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Inheritance of time of flowering in Lotus corniculatus

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INHERITANCE OF TIME OF FLOWERING IN *LOTUS CORNICULATUS*

by

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TABLE OF CONTENTS

INTRODUCTION

In the utilization of birdsfoot trefoil, Lotus corniculatus L., for pasture or hay, growth habit and time of maturity are important in determining the best management practices. Common varieties of this forage species have either upright or prostrate growth habit. In general, varieties with prostrate growth habit tend to exhibit an indeterminate vegetative growth of stems and branches whereas in those varieties with upright growth habit a cessation of stem growth is followed by a crop of secondary stems or tillers after flowering.

The variety Empire, which is a prostrate type, generally flowers about four weeks later than the Viking variety which is an upright type. A knowledge of genetic differences in flowering time is basic to studies of relationships of maturity type to such agronomic characters as forage and seed yield, longevity, seasonal growth patterns and recovery after cutting or grazing.

The primary objective of this study was to determine the nature of inheritance of flowering time in material from Empire by Viking crosses. Certain considerations were given to length of flowering stem and to seed production potential of the different maturity types studied.

LITERATURE REVIEW

A review of literature will be presented on the physiology and ecology of flowering time, the genetics of flowering time, and statistical genetics. Studies of flowering time reviewed will be chiefly those involving Lotus corniculatus L., Trifolium pratense L., and Trifolium subterraneum L. These are leguminous forage species which in general are long-day plants. Presentations will also be made from relevant studies of the short-day plant, Glycine max (L.) Merr., and of the ecotypes of Potentilla glandulosa Lindl.

Physiology and Ecology of Flowering Time

Adaptability of many species is dependent upon the reproductive process. Murneek (1948) pointed out that close adaptability to certain ecological environments may be the result of interrelationships between photoperiodism and temperature which affect growth and reproduction. Salisbury (1961) believed that if a plant responds to the length of day or night with accuracy at a given latitude then its growth and reproduction will be timed to the season and thus it will meet the requirements of natural selection. Went (1953) stated that the daily cycle of higher day and lower night temperatures, referred to as diurnal thermoperiodicity, is important in the adaptation of plants. Work with a number of species has indicated that they are strongly thermoperiodic and that cultivated varieties may differ in optimal temperatures.

In red clover, Koblet and Nüesch (1960) observed that wild plants in natural meadows of Switzerland flower independent of photoperiod but

dependent on temperature, whereas, flowering is primarily dependent on photoperiod in the well-acclimated variety, Mattenklee, which was developed from Flemish introductions. Morley and Davern (1956) showed that differences in flowering time of subterranean clover strains were related to the climate of the strain's natural habitat.

MacDonald (1946) reported on the basis of a literature review that birdsfoot trefoil is widely distributed throughout the countries of Europe. Its northern limit is about 71° north latitude and it occurs in the alpine regions of southern Europe. It is found at widely different altitudes from sea level to 10,000 feet in the Swiss Alps. Thus, in nature there must exist a great range of possibilities as to photoperiodic requirements and optimal temperatures for growth and reproduction.

Fruitfulness

Fruitfulness for a given genotype is an end product which is dependent upon growth and all phases of reproduction from floral induction to maturation of seeds. Murneek (1948) concluded from a consideration of photoperiodism that not only factors resulting in flower formation but also those that lead to failure of flowering should be studied. There are the possibilities that all available meristematic points may not be inducted due to insufficient hormone(s), many inducted points may be eliminated for lack of nutrients such as organic nitrogen, and during floral development there may be a high elimination of flowers due to competition for carbohydrates. Johnson, Borthwick and Leffel (1960) found in soybeans that the photoreaction which controls the basic reaction for floral induction appears to be essential for all other reproductive stages that follow

induction.

Abscission is defined by Addicott and Lynch (1955) as the detachment of a plant organ as a direct result of internal factors which are probably affected by temperature, water, mineral nutrients, and photoperiod. Unsuccessful competition for carbohydrates would appear to be a primary cause of flower abscission. On a clone of Viking trefoil, Winch (1958) observed sixty-eight percent flower bud abscission under a 14 hour daylength, and twenty-six percent under 16.5 hours. Under an outdoors day temperature and 45° F night temperature, Joffe (1958) observed twenty-five percent flower bud abscission for an 18 hour daylength. From his data, as presented below, increasing night temperature increased the percent flower bud abscission and reduced the number of florets per normal umbel.

Hansen (1948) found that in the transition from a vegetative to a flowering apex in birdsfoot trefoil that there was the formation of seven or eight lobes with each lobe being the primordium of a floret of the umbel. A mean number of five florets per umbel was observed. Shibles (1958) found that dalapon removal of grass competition in Viking plots resulted in no apparent increase in number of florets per umbel, whereas, the percent of flowering tillers and umbels per flowering tiller were increased.

Photoperiodic effects

Photoperiod is the daylength or period of daily illumination required for the normal growth and maturity of a plant. Salisbury (1961) generalized that a long-day plant is one which flowers in response to daylengths exceeding a minimum critical value. The response to light periods of more than the minimum value appears to be less important than the response to

the dark period, but an interaction may complicate the situation.

Ludwig, Barrales and Steppler (1953) studied the effect of photoperiod on fourteen clones of Dollard red clover under greenhouse temperatures of 65° to 75° F. All clones flowered under 16 hour daylengths, twelve under 14 hour daylengths, and none under 12 hour daylengths. Two of the clones flowered earlier and more profusely under 14 hour daylengths than under 16 hour daylengths.

Experimental results have indicated that birdsfoot trefoil is a long-day plant. Makus (1960) obtained no blooming under short-days of 8 to 10 hours, whereas daylengths of 14 hours resulted in flowering. Winch (1958) found that a clone of Viking produced flowers under 14, 14.5, and 16.5 hours of daylength but not under 9 or 11.5 hours. Joffe (1958) obtained the following results from counts made over 11 weeks on seedling-grown birdsfoot trefoil plants that were 20 weeks old and in the vegetative stage when the treatments were begun. The day and night temperatures were 69.8° and 64.4° F, respectively.

Daylength in hours	Days for appearance of normal umbels	Number of umbels formed			Percentage normal umbels
		Normal	Abortive	Total	
18	23	707	3273	3980	17.8
16	23	585	2767	3352	17.2
14	51	3	312	315	1.0

There was no difference between the 16 and 18 hour daylengths for days before appearance of normal flowers and for percentage normal flowers. However, the total number of umbels formed was greater for the 18 hour daylength. In contrast to the results of Makus (1960) and Winch (1958),

little flowering was obtained under the 14 hour daylength which indicates the possibilities of genetic differences and/or of an effect of the high night temperature in increasing the critical photoperiod.

Effects of temperature

As an environmental factor, temperature has direct, delayed, and fluctuating effects upon physiological processes of a plant and upon the plant as a whole. Went (1953) stated that most plant physiological processes function in a range from approximately 32° to 104° F, with the optimal temperatures for growth of plant parts at or above 77° F.

Little information is available on specific physiological temperatures for growth and development of such trefoil varieties as Empire and Viking. Shibles (1961) did find, under a 14 hour daylength and a temperature of 77° F in a controlled-environment room, that Viking seedlings possessed a higher relative growth rate and a greater relative leaf growth rate than Empire seedlings from the same seed size. One interpretation of such results is that Empire and Viking differ in optimal temperatures for growth. Gist and Mott (1957) studied Empire trefoil and Kenland red clover seedlings under a 12 hour daylength and controlled temperatures of 60°, 70°, 80°, and 90° F. Results at 1200 foot candles light intensity indicated that the best top and root growth for Empire trefoil was at 70° and for Kenland red clover at 60° F.

Joffe (1958) studied the effect of temperature on the flowering of birdsfoot trefoil seedlings. He obtained the following results from 7 counts over a period of 6 weeks at 18 hours daylength and a 80.6° F day temperature under controlled greenhouse conditions.

Night temperature °F	Number of umbels formed			Percentage normal flowers	Mean number of florets per normal umbel
	Normal	Abortive	Total		
45	246	403	649	37.9	3.77
64.4	207	1055	1262	16.4	3.22

On the basis of the above data, it is apparent that in comparison to 45°, the 64.4° F night temperature resulted in a considerable effect on inflorescence production. Although the total number of inflorescences was doubled, the percent of normal umbels was reduced by more than a half, and there was a reduction in the mean number of florets per normal umbel.

Red clover was studied by Roberts and Struckmeyer (1939) under long daylengths and night temperatures of 55° and 75° F. Flowering was typical under the cool temperature but was suppressed under the high temperature.

Aitken (1955) found that annual varieties of subterranean clover having a minimum cold requirement for rapid flowering were delayed in flowering by raised night temperatures. However, when increasing spring temperatures and increasing node of first flower were associated, the behavior of the latter best followed the mean rather than the minimum weekly temperatures.

The accumulation and summation of daily heat units above a specified threshold is an attempt to relate temperature with plant development toward a certain maturity stage. Such a system has many limitations as discussed by Went (1953) and Wilsie (1962).

Lindsey and Newman (1956) developed a summation method based on the daily maximum and minimum temperatures to reflect the approximate duration of different temperatures during the diurnal period. A linear growth

curve is assumed and the method excels the mean-summation method only for those days in which the temperature crosses the threshold temperature for the plant processes being studied. Temperature summations from U.S. meteorological records were applied to the spring flowering times of fourteen perennial herbs over an average of twenty-three years. The mean flowering date was 50 days after March 1, with a mean meteorological threshold temperature of 45° F, and a mean sum of 3857 degree-hours. Of the ten species that flowered before day 50, six, two, and two had threshold temperatures of 40°, 45°, and 50° F, respectively. Whereas, the four species flowering after day 50 had threshold temperatures of 50° F.

Photoperiod-temperature interactions

Lang (1952) stated that in most long-day plants the flowering response and temperature seem to be negatively related. As temperature (most decisively the night temperature) is decreased, floral initiation is promoted and the critical daylength is lowered. Thus, the increase of night temperature appears to increase an inhibitory effect of the dark period within a normal range of temperature.

Similar results were obtained by Evans (1959) in a study of vernalized and unvernalized plants of early and late strains of subterranean clover. Under continuous light a rise in mean temperature from 54.1° to 77.5° F resulted in a reduction in the time before floret appearance. However, flowering under 16-hour photoperiods was later than under continuous light and was further delayed by a rise in temperature above 66.2° F. Thus, high temperatures in the dark period have an inhibitory effect on flowering, which may in turn mask the accelerating effect of higher temperatures

during the light period. The latest flowering strain gave the greatest response to the two promotive processes (vernalization and high photo-temperatures) and to the one inhibitory process of the dark period, whereas the earliest strain gave the least response.

Fergus and Hollowell (1960) reported that vegetative growth was reduced and flowering was earlier when a Louisiana variety of red clover from 31° latitude was grown under the temperature and daylength conditions of 38° latitude in Kentucky, indicating a temperature-daylength interaction.

Flowering hypothesis for birdsfoot trefoil

On the basis of the above literature review, a working hypothesis for time of flowering in birdsfoot trefoil may be formulated as a background against which to interpret genetic data. Such varieties as Empire and Viking are assumed to be long-day plants. It is postulated that flower initiation and development is controlled by the interactions of photoperiod, temperature, and the genetically controlled physiological mechanisms of the plant. In general, flowering is favored by long daylengths, high day temperatures and low night temperatures. However, any given genotype may have its own unique requirement for photoperiod and temperature. Under natural conditions the lower the photoperiodic requirement of a genotype the greater the probability of a day and night temperature interaction which will accelerate flowering, and the higher the photoperiodic requirement of a genotype the greater the probability of a day and night temperature interaction which will delay flowering.

The germplasm from which the varieties Empire and Viking were developed must have arisen in response to natural selection under different

ecological conditions. Empire has a more prostrate growth habit and is more indeterminate in growth and flowering than Viking. In comparing overwintered plants, both varieties may have similar physiological threshold temperatures for growth but different optimal growth temperatures especially in comparison to temperatures promoting flowering. In Empire, if optimal growth temperatures are less than in Viking, growth may be favored over flowering in the spring until less optimal temperatures for growth are reached in the summer, photoperiodic requirements are met, and/or the potential amount of growth for that genotype is approached. Whereas, if in Viking the photoperiodic requirements are less, the optimal growth temperatures higher, and the genetic potential for indeterminate growth prior to flowering less than in Empire, earlier but more determinate flowering would be favored.

Genetics of Flowering Time

According to Teas (1957) there are many plants in which differences in maturity date have been concluded to be due to a single gene or a small number of genes. As an example, Clausen and Hiesey (1958, p. 193) reported that the F_2 from a cross of a spring-blooming race and a fall-blooming race of Madia elegans indicated the presence of a dominant, epistatic gene causing early flowering, and of two cumulative genes, causing late flowering, that were hypostatic to the gene for earliness. Teas (1957) stated that genetic differences in flowering time may involve variations in photoperiod response or in earlier photoinductive sensitivity, and Barber (1959) believed that the adaptive control of flowering

could have been arrived at through several different genetic systems.

In a cross of a wild red clover with the variety Mattenklee, Koblet and Nüesch (1960) observed the non-photoperiodic earliness of the former to be almost completely dominant in the F_1. However, in the F_1 from three crosses of late flowering, introduced parents with Mattenklee, the photoperiod-dependent earliness of Mattenklee was partially dominant. Rinke and Johnson (1941) observed transgressive segregation for earliness and lateness of flowering in an F_2 population of red clover.

Davern, Peak and Morley (1957) studied strains of subterranean clover and hybrids among them under field conditions which permitted vernalization. Heterosis and dominance were not observed and the genetic variation was quantitative. All F_1 means and almost all F_2 means were very similar to their respective midparent values.

Poostchi (1960) stated that in New York the flowering periods of Viking and Empire trefoil are typically the first two weeks of June and July, respectively. He concluded from varietal crosses that the early flowering habit of Viking was dominant over the late flowering habit of Empire.

Clausen and Hiesey (1958) studied flowering time in Potentilla glandulosa by crossing a subalpine ecotype from Timberline with a foothills ecotype from Oak Grove. Clonal propagules of 511 F_2 plants were observed for four years at three transplant stations, Stanford (30 m.), Mather (1400 m.), and Timberline (3050 m.). There was considerable transgressive segregation but its extent and direction as compared to the parents differed in the three contrasting environments. There was a

year-to-year consistency at any one station for order of flowering time among the F_2 plants but there was considerable difference in response over the three stations resulting in a non-significant station-to-station correlation in earliness of flowering. It was concluded that differences in earliness of flowering in contrasting ecotypes are governed by complex systems of genes, that such genes are expressed through processes greatly influenced by environment, and that distinct sets of genes may become activated in different environments.

The possibility that any two similar phenotypes may owe their likeness to different genes or combinations of genes is considered by Mather (1949, p. 24). As presented by Clausen and Hiesey (1958, p. 148), of the 64 F_2 plants that flowered in the earliest group at Stanford, 30 plants flowered in the intermediate group at Mather. However, these plants, which were of similar phenotype at Mather and Stanford, were distributed into groups over the complete range of flowering-time phenotypes at Timberline. This transplant method provides the means of separating similar flowering-time phenotypes into groups. Another transplant cycle using the progeny from such phenotypically separated groups would yield information about genetic systems. Such studies are needed to permit generalization about different genetic systems producing similar flowring-time phenotypes under a similar environment, and to provide genetic information basic to the interpretation of genotype-environment interactions.

Genotype-environment interactions have been observed for flowering time in subterranean clover. Morley and Davern (1956) observed that the

order of flowering time of varieties grown in a number of locations might differ from location to location. These interactions were interpreted in terms of the effects of photoperiod and low temperature on flowering. Davern, Peak and Morley (1957) observed a small but significant strain by year interaction when strains were grown in two years.

Statistical Genetics

The heritable and non-heritable variation of a character may be expressed in terms of the phenotype. The variance of the phenotype is given by:

$$V_P = V_G + V_E + 2_{cov(G,E)}$$

where V_G is genetic variance, V_E is environmental variance, and $2_{cov(G,E)}$ is covariance of genotypic values and environmental deviations. Additivity of genetic causes and environmental causes generally is assumed and is validated by randomization of individuals in the experiment. However, if $2_{cov(G,E)}$ does not equal zero in practice, Falconer (1961) pointed out that such covariance arising from genotype-environment correlation will appear as a part of the genetic variance.

There are a considerable number of theoretical and experimental studies of quantitative genetics, some of which are reviewed and discussed by Allard (1960). Many of the studies pertain to diploid populations in which gene frequency can be assumed to be one-half. Such studies are not specifically applicable to the present study for two reasons. Homozygous lines of birdsfoot trefoil are not available, thus assumptions of gene frequencies of one-half cannot be made. As reported previously (Buzzell,

1960), the evidence indicates that inheritance in trefoil is tetrasomic, thus variances and covariances should be considered from an autotetraploid standpoint.

The general case of a random mating, autotetraploid population with variable alleles at each locus was considered by Kempthorne (1955). An individual possesses for one locus, 4 variable additive (simplex) gene effects, 6 dominance or digenic (duplex) contributions, 4 trigenic (triplex) contributions and 1 quadrigenic (quadriplex) contribution. In the case of two variable loci, the above contributions are doubled to 8, 12, 8, and 2 contributions, respectively, plus 225 interaction terms which contribute to the genotypic value. Li (1955) considered the special case of only two kinds of alleles at a locus. In this case the total genotypic variance is as follows:

Diploid $\sigma_G^2 = \sigma_A^2 + \sigma_D^2$

Autotetraploid $\sigma_G^2 = \sigma_A^2 + \sigma_D^2 + \sigma_T^2 + \sigma_F^2$

where A and D are additive (monogenic) and dominance (digenic) contributions, respectively, and T and F are for the trigenic and quadrigenic contributions, respectively.

Kempthorne (1955) demonstrated in the autotetraploid case that neither the parent-offspring nor the half-sib genotypic covariance contains trigenic and quadrigenic terms. However, full-sib genotypic covariance contains 1/2 of the additive, 2/9 of the dominance, 1/12 of the trigenic, and 1/36 of the quadrigenic contributions. Thus, an analysis of half-sib and full-sib families, as presented by Falconer (1961, p. 172) to estimate additive and dominance components, is not applicable to autotetraploids.

An empirical study as suggested by Kempthorne (1955) involving different types of matings and the testing of observed covariances against expected covariances would be needed to obtain estimates of the additive, dominance, trigenic, and quadrigenic components. Such a study would necessitate a very large number of plants.

Pergament and Davis (1961) partitioned the heritable variances of mature plant height in alfalfa into additive and nonadditive (dominance) components on a disomic and tetrasomic basis. Their results gave the better fit to the tetrasomic model in which it was assumed that all loci affecting height were triplex in one parent and simplex in the other. The assumed gene frequencies of .75 and .25 are quite arbitrary.

Comstock and Robinson (1952) suggested that the use of covariance between half-sib families and parent clones appeared to be the best basis available for estimating variance due to average gene effects in polyploid species. They also presented general information for estimating genetic parameters.

The separation of genetic and environmental effects is desired in order to remove the masking effect of the environment and permit selection on a genetic basis. Hazel and Lush (1942) stated that in order to select most efficiently, the relative economic value of each trait, its heritability, and the genetic and environmental correlations of each trait with other characters should be known.

Heritability has been reviewed by Burton (1952) and by Hayes, Immer and Smith (1955, Chapter 12). Johnson, Robinson and Comstock

(1955) stated that an estimate of heritability based on a single experiment is an estimate of the genetic variance plus interaction (genotype by locations and genotype by years) variances to phenotypic variance.

MATERIALS AND METHODS

Clonal and segregating material of birdsfoot trefoil was studied in space-planted field experiments at the Agronomy Farm in Ames at 42° north latitude. The plants were spaced two feet apart within forty-inch rows in fields which were about one-half mile south of the cooperative U.S. weather station.

Origin of Breeding Materials

The original genetic material was obtained from the forage breeding program at Iowa State University. The selections were as follows:

Late flowering

533 F_2 plant from Viking x Empire cross (V-2 x E-2)

540 F_2 plant from Viking x Empire cross (V-2 x E-2)

567 F_2 plant from Viking x Empire cross (V-2 x E-7)

E-7 Empire plant

Early flowering

578 Viking plant (52-3)

579 Viking plant (52-9)

2186 Plant from a Swiss introduction; completely pollen sterile.

Each of the late-flowering plants was crossed to each of the early-flowering plants, giving 12 F_1 progenies. Six F_1 plants were selected at random out of the four families of 533, 540, 567, and E-7 by 578. The six F_1 sib-selections within each family were combined in a chain cross series as follows, 1 x 2, 2 x 3, 3 x 4, 4 x 5, 5 x 6, and 6 x 1.

The even number of selections resulted in an even number of crosses and permitted the separation of the F_2 progenies into two groups as follows:

Group A 1 x 2, 3 x 4, and 5 x 6

Group B 2 x 3, 4 x 5, and 6 x 1

These groups were designated as half-sib groups within each family. F_2 families were designated as having arisen from the crosses 533 x 578, 540 x 578, 567 x 578 and E-7 x 578.

A similar group of 24 F_1 plants that were selected at random out of the families involving 2186 had to be discarded because most of them were pollen sterile.

Experimental Procedures

The field and greenhouse techniques for plant propagation, crossing, and handling of experimental material were the same as described previously (Buzzell, 1960). Plants were established and allowed to overwinter prior to making flowering-time observations in order to eliminate any possible differences in short day and/or cold requirements for flowering.

The F_1 progenies were transplanted May 27, 1959, into a randomized block design of three replications in field 900C. The F_2 progenies were transplanted into a 4 x 4 Latin square design during June 1960, in field 1400C. The four F_2 families were assigned at random to blocks. Each family block contained seven two-row plots. Each row had 16 plants per row, plus one or two border plants of the same material.

The six F_2 progenies and a clonal entry of the family were assigned

at random to the seven plots of a family block. The clonal entry was made up of eight parental clones, that is, the early and late-flowering parents and the 6 F_1 sib-selections for that family. Within each row of a clonal plot, clones were assigned at random to hill plots of two propagules.

Measurement of Characters Studied

During the flowering period in the spring and summer of 1960, observations were made of flowering on every day that weather conditions permitted. A plant was recorded as flowering when the florets of an umbel were fully opened. The time of flowering in days after May 12 was recorded for the first, second, and third umbels. May 12 was used as a point of origin because it appeared to be the earliest date that flowering could begin in this species at this location. When flowering of an umbel was recorded, the number of florets for that umbel also was noted. Approximately six weeks after each plant began flowering, it was rated on a scale of five to nine for seed pod production. On the rating scale five was good and included those that might have been rateable as one, two, three or four, and nine was very poor.

Observations of flowering time were made approximately every three days during the flowering period in the spring and summer of 1961. The time of flowering was estimated and recorded in days after May 12. When flowering was recorded, the length of the flowering stem of that plant was measured in inches and recorded as plant height.

Statistical Procedures

Observations of flowering time were analyzed as days after May 12, 1960 and May 12, 1961. Mather and Vines (1952) stated that as long as a transformation was not made, one date was as good as another as the point of origin. As will be shown later, analyses of data based on standard degree-days would facilitate in comparing years and in making combined analyses in this species.

The standard procedures in Snedecor (1956) and Cochran and Cox (1957) were followed in doing analyses of variance and covariance, making orthogonal comparisons, and computing Least Significant Bounds based on Duncan's Multiple Range Test.

Each L.S.B. was obtained as the difference between the mean of an entry and its corresponding shortest significant range (R_p) in the Multiple Range Test. Necessarily the lowest ranking mean will have no L.S.B. If the mean of an entry is less than the L.S.B. of another entry, it is considered to be significantly different at the .05 probability level.

Heritabilities were computed by each of three general methods. Thomas and Kernkamp (1954) served as a reference in the method which utilized variance components from an analysis of variance. Snedecor (1956) was followed in computing midparent-progeny regressions. Information from Mather (1949) was used in obtaining estimates of genetic variance in F_2 progenies by subtracting non-heritable, clonal variance from the F_2 variance.

The report of Comstock and Robinson (1952) was followed in equating

mean squares with their expectations in terms of variance components and solving for the components. Covariance components were obtained in an analogous manner from the covariance analyses.

Hoover (1952) and Peacock and Wilsie (1960) served as references in the path and correlation coefficient analyses. The environmental, genetic, and observed correlations were obtained by dividing the respective covariance with the geometric mean of the corresponding variances.

The procedure used to obtain a genetic coefficient of variation, as proposed by Burton (1952), was to divide the square root of the genetic variance by the mean, followed with multiplication by 100.

EXPERIMENTAL RESULTS

The experimental results are presented under the topics of F_1 results for 1960, an integration of 1960 and 1961 results, the results of individual F_2 progenies in 1961, heritability estimates and genetic advance, correlation analysis, and experimental precision and efficiency.

F_1 Results for 1960

Observations were made of flowering time and number of florets for the first three umbels to bloom. Each plant was rated for seed production potential approximately six weeks after it first flowered. These F_1 data were utilized for comparisons of parental differences in average combining ability. Comparisons of 578, 579 and 2186 are averages over four crosses, but the three comparisons of 533, 540, 567 and E-7 are based on a single cross to 578, 579 or 2186 in order to provide information on the families from 578 which were studied in the F_2. However, the three sets of comparisons may be visually averaged in the tables.

The means for flowering time of the first, second, and third umbels of the parents and F_1 progenies appear in Table 1. The analysis of variance of flowering time presented in Table 2, shows no significant differences within progenies for first, second, and third umbels. The umbels-within-progenies mean square was smaller than the rows-within-plots mean square indicating that the within-plant variability was comparatively small in this material. The among-progenies mean square was significant at the .01 probability level and orthogonal comparisons of the parents were made on a progeny basis. In the comparisons of early-flowering

Table 1. Flowering-time means in days after May 12, 1960 for the first, second, and third umbels, mean seed production ratings, and mean number of florets per umbel for F_1 progenies and parents

	No. of plants	Flowering-time means in days after May 12, 1960			Mean seed production ratings[a]	Mean number of florets per umbel
		1st umbel	2nd umbel	3rd umbel		
F_1 progenies						
533 x 578	46	19.8	20.9	21.4	7.1	4.5
540 x	46	12.3	12.7	13.1	6.2	5.3
567 x	46	12.0	12.6	13.1	6.3	4.8
E-7 x	52	13.8	14.3	14.7	5.3	5.6
533 x 579	48	17.0	18.6	19.3	6.4	4.5
540 x	50	11.4	12.2	12.6	5.9	5.3
567 x	49	12.8	13.7	14.1	6.2	4.8
E-7 x	50	15.9	16.8	17.1	5.4	5.4
2186 x 533	52	9.6	10.6	11.0	5.9	4.3
x 540	49	7.8	8.5	9.0	5.4	4.7
x 567	46	5.8	6.8	7.4	5.2	4.3
x E-7	49	11.8	12.7	13.3	5.4	4.7
Parents						
533	15	37.7	38.5	38.7	-	5.0
540	12	29.3	34.8	38.5	-	4.4
567	14	30.4	33.1	33.4	-	4.8
E-7	3	34.3	35.0	35.7	-	4.9
578	12	10.8	11.3	11.5	-	4.8
579	14	4.6	5.1	5.3	-	4.4
2186	6	2.3	4.3	5.0	-	3.5

[a]5 is good, 9 is very poor.

Table 2. Analysis of variance of F_1 progenies for flowering time of the first three umbels per plant, with orthogonal comparisons of the parents on a progeny basis

Source of variation	Mean flowering times of comparisons in days after May 12, 1960		D.F.	Flowering time mean squares
Replications			2	9.69
Progenies			11	278.81**
Umbels within progenies			24	2.98
Error			70	5.40
Rows within plots			108	3.74
Comparisons of progenies from crosses with				
578 and 579 vs. 2186	15.1	9.5	1	1,480.74**
578 vs. 579	15.1	15.1	1	.05
533,540 and 567 vs. E-7	15.3	14.3	1	15.52
578 533 and 540 vs. 567	16.7	12.6	1	203.36**
533 vs. 540	20.7	12.7	1	579.20**
533, 540 and 567 vs. E-7	14.6	16.6	1	52.51**
579 533 and 540 vs. 567	15.2	13.5	1	32.67*
533 vs. 540	18.3	12.0	1	352.19**
533, 540 and 567 vs. E-7	8.5	12.6	1	222.04**
2186 533 and 540 vs. 567	9.4	6.7	1	92.41**
533 vs. 540	10.4	8.4	1	36.20*

*Significant at the .05 probability level.

**Significant at the .01 probability level.

parents, the Swiss plant 2186 differed from the Viking parents, 578 and 579 in early-flowering combining ability at the .01 probability level. In comparing late-flowering parents in crosses by 578, E-7 did not differ in late-flowering combining ability from the average of 533, 540 and 567. However, 533 differed at the .01 probability level from 540. All comparisons involving 533, 540, 567 and E-7 in crosses by 579 and 2186 for differences in late-flowering combining ability were significant.

The F_1 progeny means for seed-production ratings appear in Table 1 and the corresponding analysis of variance is presented in Table 3. Progenies differed at the .01 probability level and orthogonal comparisons were made for combining ability for seed production. The parent 2186 was better at the .01 probability level in combining ability for seed production than the average of the parents 578 and 579. In crosses to both 578 and 579, the late-flowering parent E-7 was better at the .01 probability level in combining ability for seed production than the average of 533, 540 and 567. It is concluded that of the early-flowering parents, 2186 has the best combining ability for seed production, and of the late parents, E-7.

The mean number of florets per umbel, using the first three flowering umbels on each plant observed, are given in Table 1 for the F_1 progenies and parents. In the analysis of variance, presented in Table 4, the progenies differed at the .01 probability level and orthogonal comparisons of number-of-florets combining ability were made. The parent 2186 was poorer at the .01 probability level in number-of-florets combining ability than 578 and 579. In crosses to 578 and 579, the parent 533 was poorer at the

Table 3. Analysis of variance of F_1 progenies for seed-production ratings, with orthogonal comparisons of the parents on a progeny basis

Source of variation	Mean seed production ratings of comparisons		D.F.	Seed production rating mean squares
Replications			2	.23
Progenies			11	1.02**
Comparisons of progenies from crosses with				
578 and 579 vs. 2186	6.0	5.4	1	3.38**
578 vs. 579	6.2	6.0	1	.43*
578: 533, 540 and 567 vs. E-7	6.5	5.3	1	3.30**
578: 533 and 540 vs. 567	6.6	6.3	1	.20
578: 533 vs. 540	7.1	6.2	1	1.40**
579: 533, 540 and 567 vs. E-7	6.2	5.4	1	1.48**
579: 533 and 540 vs. 567	6.2	6.2	1	.00
579: 533 vs. 540	6.4	5.9	1	.38
2186: 533, 540 and 567 vs. E-7	5.5	5.4	1	.03
2186: 533 and 540 vs. 567	5.6	5.2	1	.29
2186: 533 vs. 540	5.9	5.4	1	.38
Error			22	.09

*Significant at the .05 probability level.

**Significant at the .01 probability level.

Table 4. Analysis of variance of F_1 progenies for number of florets per umbel, with orthogonal comparisons of the parents on a progeny basis

Source of variation	Mean number of florets per umbel of comparisons		D.F.	Florets per umbel mean square
Replications			2	.05
Progenies			11	.58**
Comparisons of progenies from crosses with				
578 and 579 vs. 2186	5.0	4.5	1	2.09**
578 vs. 579	5.0	5.0	1	.02
578 533, 540 and 567 vs. E-7	4.5	5.2	1	1.03**
578 533 and 540 vs. 567	5.3	5.2	1	.01
578 533 vs. 540	4.8	5.6	1	1.04**
579 533, 540 and 567 vs. E-7	4.5	5.2	1	.64
579 533 and 540 vs. 567	5.3	5.1	1	.04
579 533 vs. 540	4.8	5.4	1	.88**
2186 533, 540 and 567 vs. E-7	4.3	4.6	1	.25
2186 533 and 540 vs. 567	4.7	4.5	1	.08
2186 533 vs. 540	4.3	4.8	1	.33
Error			22	.08

**Significant at the .01 probability level.

.01 probability level in number-of-florets combining ability than 540. The parent E-7 was better at the .01 probability level in combining ability for number of florets than the average of 533, 540, and 567 in the crosses to 578 but not in the crosses to 579.

In conclusion, the following results would be expected in the F_2 of families of the four late-flowering parents crossed to 578. The flowering-time mean of the E-7 family should not be later than the average of the 533, 540 and 567 families. The mean seed production and number of florets per umbel of the E-7 family should be better than the average of the 533, 540 and 567 families. The mean seed production and number of florets per umbel in the 533 family should be poorer than in the 540 family.

Integration of 1960 and 1961 Results

In 1961 observations for flowering time and height (length of flowering stem) at time of flowering were made on parental, F_1 and F_2 material. The flowering-time and height means of the parents, 578, 533, 540, 567 and E-7, are given in Table 5. The early-flowering parent, 578, varied as much as 3.0 days in flowering time and 1.9 inches in height over blocks. The range in variation among the four late-flowering parents was only 3.3 days for flowering time but was 8.3 inches for height. It appeared that 540 and 567 made less growth than 533 and E-7 in a similar period of time. Also included in Table 5 are the means for flowering time and height of the F_1 sib-parents, and the Least Significant Bound for flowering time and height of each clone as calculated using the standard errors from the analyses of variance in Appendix Table 34. Only in the E-7 x 578 family

Table 5. Means of parental clones for flowering time and height of flowering stem, with the respective Least Significant Bound for each mean within a family

	No. of propagules	Flowering time in days after May 12, 1961		Height in inches at flowering time	
		Mean[a]	L.S.B.	Mean	L.S.B.
Family 533 x 578					
533	16	38.6	34.8	18.0	16.7
578	17	20.4	16.9	9.5	-
F_1 Sib-1	18	26.0	22.3	18.5	16.7
2	19	20.0	16.6	14.7	13.1
3	17	26.7	22.9	15.4	13.7
4	17	22.2	18.6	16.4	14.7
5	17	26.8	23.0	17.6	15.8
6	16	18.1	-	13.6	12.0
Family 540 x 578					
540	16	38.9	31.9	13.4	11.8
578	17	17.4	11.3	10.0	8.5
F_1 Sib-1	13	28.7	21.8	9.5	-
2	17	23.4	16.5	9.6	8.2
3	16	16.1	-	10.5	8.9
4	16	18.4	12.0	12.8	11.2
5	16	20.7	14.1	11.1	9.5
6	19	22.5	15.7	11.0	9.4

[a]For comparison with 1960 data, subtract 7 days.

Table 5 (Continued).

	No. of propagules	Flowering time in days after May 12, 1961		Height in inches at flowering time	
		Mean[a]	L.S.B.	Mean	L.S.B.
Family 567 x 578					
567	11	41.5	38.8	11.1	11.7
578	19	17.4	-	11.2	-
F_1 Sib-1	17	21.0	18.3	13.5	11.7
2	16	18.0	15.5	10.2	8.6
3	17	19.4	16.8	10.0	8.4
4	15	17.5	15.1	11.5	9.8
5	16	25.2	22.5	12.4	10.6
6	17	19.7	17.1	8.2	-
Family E-7 x 578					
E-7	14	38.2	32.4	19.4	16.9
578	17	19.6	-	9.3	-
F_1 Sib-1	10	34.4	28.7	17.6	15.2
2	18	24.0	18.4	15.8	13.4
3	17	20.3	15.0	12.4	10.2
4	17	35.6	29.8	18.8	16.3
5	16	22.1	16.6	14.2	11.8
6	16	19.8	14.7	13.3	11.0

are there F_1 sib-selections which are not earlier in flowering time than the Least Significant Bound of the late-flowering parent.

The analysis of variance for flowering time and height, presented in Tables 6 and 7, indicate that there are significant differences among families of parental clones. The significant differences in the set of orthogonal comparisons of flowering time in Table 6 are not the same as those in the corresponding set of comparisons in Table 2. The E-7 clonal family is significantly later at .01 probability level than the average of the 533, 540, and 567 families. Whereas in the F_1 populations, the E-7 family had not differed significantly from the average of the 533, 540, and 567 families, however, the 567 family and the 540 family were significantly earlier at the .01 probability level than the average of the 533 and 540 families and the 533 family, respectively.

All the orthogonal comparisons for height among families of parental clones in Table 7 were significant at the .01 probability level. The midparent values and F_1 means for height in Table 8 are in agreement with this clonal data in which the 533 and E-7 families are taller than the 540 and 567 families.

The F_1 progeny means and midparent values obtained for flowering time in 1961 appear in Table 8. The F_1 means ranked in the same order as those obtained in 1960 but on the average flowering was estimated to be a week later. This estimate is supported by the differences in number of heat degree-hours computed from Climatological Data, Iowa (1960, 1961) by the method of Lindsey and Newman (1956). The summations above a base temperature of 40° F, as presented in Table 9, indicate that not quite as many

Table 6. Analysis of variance of flowering time for families containing eight parental clones, with orthogonal comparisons of the families

Source of variation		Mean flowering time[a] of comparisons in days after May 12, 1961		D.F.	Flowering time mean squares
Rows				3	18.67
Columns				3	63.13
Families				3	123.53*
Comparisons of families					
	533, 540 and 567 vs. E-7	23.6	27.0	1	278.80**
578	533 and 540 vs. 567	24.1	22.5	1	53.98
	533 vs. 540	24.9	23.3	1	37.82
Error				6	17.22

[a]For comparison with 1960 data, subtract 7 days.

*Significant at the .05 probability level.

**Significant at the .01 probability level.

Table 7. Analysis of variance of height of flowering stem for families containing eight parental clones, with orthogonal comparisons of the families

Source of variation	Mean height of comparisons in inches		D.F.	Mean squares for height of flowering stem
Rows			3	6.96
Columns			3	.98
Families			3	195.89**
Comparison of families				
533, 540 and 567 vs. E-7	12.5	15.1	1	164.33**
578 533 and 540 vs. 567	13.2	11.0	1	104.28**
533 vs. 540	15.4	11.0	1	319.07**
Error			6	3.73

**Significant at the .01 probability level.

Table 8. F_1 progeny means and midparent values for flowering time and height at time of flowering in 1961

	No. of F_1 plants	Flowering time in days after May 12, 1961		Height of flowering stem in inches	
		Midparent[a]	Mean[a]	Midparent	Mean
533 x 578	16	29.1	30.0	13.8	16.1
540 x 578	15	28.0	18.5	11.6	13.3
567 x 578	17	29.8	19.4	11.2	13.3
E-7 x 578	17	29.3	21.4	14.4	15.9

[a]For comparison with 1960 data, subtract 7 days.

Table 9. Air and soil temperature degree-hours for the spring of 1960 and 1961 summed above a 40° F base temperature using daily maximum and minimum temperatures from Climatological Data, Iowa (1960, 1961)

Weeks ending	Accumulative degree-hours			
	Air temperature at 4 feet		Soil temperature at 8 inches	
	1960	1961	1960	1961
April 7	562	222	0	95
14	2296	833	590	350
21	4697	2266	2150	1084
28	8183	4136	5006	3040
May 5	10964	5537	7382	4984
12	12739	8780	9638	7648
19	16627	11972	13322	11032
26	20491	15059	17354	14644
June 2	24751	19367	21374	19132
9	28963	24047	26174	24100
16	33799	29111	30914	29452
23	38455	33227	35798	34612
30	43351	38687	41186	40574

air temperature degree-hours had accumulated by May 19, 1961, as had accumulated by May 12, 1960. A comparison of soil temperature degree-hours indicates that the May 12, 1961 accumulation was about equal to the May 5, 1960 accumulation. Thus, days after May 19, 1961, appear to be comparable to days after May 12, 1960. However, the data were analyzed within each year as days after May 12 and not in standard degree days.

The percentage distributions of parental, F_1, and F_2 plants with first bloom expressed in weeks after May 12, 1960 and May 19, 1961, are given in Table 10 along with means in comparable days. In the 533, 540, 567 and E-7 by 578 F_1 families respectively, 23, 84, 73, and 58 percent of the plants flowered in the second week. Whereas in the respective F_2 families, 17, 66, 54 and 28 percent of the plants flowered in the second week. In the same order, 16, 0, 3, and 1 percent in the F_1 families, and 33, 6, 7, and 19 percent of the F_2 families flowered in the fourth week.

The F_2 family means were later than the F_1 family means, ranging from 1.4 days later for family 533 x 578 to 6.6 days later for family E-7 x 578. In the latter family, the shift is due to a reduction in percentage of F_2 plants flowering in the second week and an increase in the fourth and following weeks.

There was considerable variation present in many of the clones, indicating a substantial environmental effect. Thus, the F_2 distributions do not appear suitable for a graphical analysis in terms of arithmetic probability to separate sub-populations such as Donovan (1959) did for leaf size in trefoil. Burton (1952) stated that it was pointless to use unimodality, normality, or smoothness of F_2 distributions as indicators

Table 10. Percentage frequency distributions within four families for parental, F_1 sib-parental, F_1, and F_2 plants with first bloom in weeks after May 12, 1960 and May 19, 1961

	No. of plants	Percentage plants with first bloom in weeks after May 12, 1960 and May 19, 1961								Mean in comparable days
		1	2	3	4	5	6	7	8	
Family 533 x 578										
Clone 533	16	-	-	-	25.0	43.8	31.2	-	-	31.6
578	17	-	82.3	11.8	5.9	-	-	-	-	13.4
F_1 Sib-1	18	-	-	66.7	33.3	-	-	-	-	19.0
2	19	-	89.5	10.5	-	-	-	-	-	13.0
3	17	-	23.5	35.4	23.5	17.6	-	-	-	19.7
4	17	-	41.2	58.8	-	-	-	-	-	15.2
5	17	-	-	76.5	23.5	-	-	-	-	19.8
6	16	-	100.0	-	-	-	-	-	-	11.1
Population F_1	62	-	22.6	41.9	16.1	11.3	3.2	4.8	-	21.3
F_2	753	-	16.7	29.5	33.1	10.9	7.0	2.4	0.4	22.7
Family 540 x 578										
Clone 540	16	-	-	6.2	37.5	25.0	6.2	25.0	-	31.9
578	17	5.9	94.1	-	-	-	-	-	-	10.4
F_1 Sib-1	13	-	30.8	30.8	15.4	-	23.1	-	-	21.7
2	17	-	64.7	11.8	17.6	-	5.9	-	-	16.4
3	16	12.5	87.5	-	-	-	-	-	-	9.1
4	16	6.2	93.8	-	-	-	-	-	-	11.4
5	16	-	81.3	6.2	12.5	-	-	-	-	13.7
6	19	-	52.6	47.4	-	-	-	-	-	15.5
Population F_1	61	-	83.6	16.4	-	-	-	-	-	12.4
F_2	746	1.9	65.5	18.5	5.9	3.5	2.8	1.2	0.7	15.4

Table 10 (Continued).

	No. of plants	Percentage plants with first bloom in weeks after May 12, 1960 and May 19, 1961								Mean in comparable days
		1	2	3	4	5	6	7	8	
Family 567 x 578										
Clone 567	11	-	-	-	18.2	27.3	54.5	-	-	34.5
578	19	5.3	95.7	-	-	-	-	-	-	10.4
F_1 Sib-1	17	-	70.6	29.4	-	-	-	-	-	14.0
2	16	-	93.8	6.2	-	-	-	-	-	11.0
3	17	-	88.2	11.8	-	-	-	-	-	12.4
4	15	13.3	66.7	20.0	-	-	-	-	-	10.5
5	16	-	6.2	81.3	12.5	-	-	-	-	18.2
6	17	-	70.6	29.4	-	-	-	-	-	12.7
Population F_1	63	1.6	73.0	22.2	3.2	-	-	-	-	12.7
F_2	799	2.1	53.6	29.9	7.4	3.6	2.9	0.5	-	15.4
Family E-7 x 578										
Clone E-7	14	-	-	-	28.6	71.4	-	-	-	31.2
578	17	-	88.2	11.8	-	-	-	-	-	12.6
F_1 Sib-1	10	-	-	10.0	60.0	20.0	-	10.0	-	27.4
2	18	-	5.6	88.8	5.6	-	-	-	-	17.0
3	17	-	76.4	23.6	-	-	-	-	-	13.3
4	17	-	11.8	-	35.3	35.3	17.6	-	-	28.6
5	16	-	43.8	50.0	6.2	-	-	-	-	15.1
6	16	-	87.5	12.5	-	-	-	-	-	12.8
Population F_1	69	1.4	58.0	37.7	1.4	1.4	-	-	-	14.3
F_2	743	0.1	28.3	34.6	19.0	8.5	7.0	1.9	0.7	20.9

of number of genes when there is considerable environmental variation present.

Environmental variation also appeared to have an effect upon estimates of transgressive segregation as shown in Table 11. If the mean of the early parent is used, transgressive segregation for earliness ranged from 9.4 to 12.9 percent of the population and from 4 to 8 days in extent. However, if only those F_2 plants that flowered before the earliest propagule are considered the percentages range from 0.4 to 2.2 and the extent from 2 to 4 days. In a similar manner, transgressive segregation for lateness which ranged from 3.1 to 15.6 percent and from 13 to 21 days in extent was reduced to a range of 0.5 to 9.6 percent and of 5 to 17 days in extent.

The E-7 x 578 family yielded the high estimates of 9.6 percent and 17 days in extent for late-flowering transgressive segregation apparently as a result of the fact that propagules of E-7 exhibited less environmental variability than those of 533, 540 and 567. These latter three parents are F_2 plant selections from Empire by Viking crosses, which points out the fact that many late-flowering transgressive segregants may be late-flowering only because they are more subject to environmental variation than adapted late-flowering plants of Empire. It should be noted that propagules of the Viking parent, 578, varied in flowering (over blocks) from day 11 to day 30.

The analysis of variance of means for flowering-time of the F_2 families appears in Table 12. In the usual comparisons, the E-7 F_2 family was later at the .05 probability level, and the 567 and 540 F_2 families were earlier at .01 probability level. That the F_1 and F_2

Table 11. Early and late-flowering transgressive segregation of F_2 families expressed in percent of the population and in extent of days earlier and later than the mean and range of the respective early and late flowering parents

F_2 Populations	Percent of population earlier than		Percent of population later than		Extent of days earlier than		Extent of days later than	
	Range of early parent	Mean of early parent	Range of late parent	Mean of late parent	Range of early parent	Mean of early parent	Range of late parent	Mean of late parent
Family 533 x 578	1.7	9.4	3.7	15.5	2	4	11	19
Family 540 x 578	0.4	11.0	0.9	5.9	2	8	5	19
Family 567 x 578	0.5	11.6	0.5	3.1	2	6	6	13
Family E-7 x 578	2.2	12.9	9.6	15.6	4	7	17	21

Table 12. Analysis of variance and orthogonal comparisons of flowering-time means of F_2 families

Source of variation	Mean flowering time[a] of comparisons in days after May 12, 1961		D.F.	Flowering time mean squares
Rows			3	21.17
Columns			3	170.81*
Families			3	686.49**
Comparison of families				
533, 540 and 567 vs. E-7	24.8	27.9	1	345.80*
578 533 and 540 vs. 567	26.0	22.4	1	417.84**
533 vs. 540	29.7	22.3	1	1,295.80**
Error			6	27.87

[a]For comparison with 1960 data, subtract 7 days.

*Significant at the .05 probability level.

**Significant at the .01 probability level.

families from 540 and 567 were similar and earlier than the F_1 and F_2 families from 533 and E-7, might be expected. The crosses of 533, 540, and 567 to 578 are in essence varietal backcrosses to Viking. Although late flowering, the parents 540 and 567 are somewhat typical of Viking, whereas 533 is definitely atypical. As was discussed previously both the parents and their F_1 progenies differed in height at flowering time. In the usual comparisons as presented in Table 13, the 567 and 533 F_2 families were shorter at the .01 probability level.

Results of Individual F_2 Progenies, 1961

The parental and midparental means of flowering time for the F_1 sib-matings which gave the F_2 populations within each family are presented in Table 14. The earlier parent differed from the Least Significant Bound (.05 probability level) of the later parent, in all six of the matings in family 533 x 578, in two of the six matings in family 540 x 578, in three of the six matings in family 567 x 578, and in four of the six matings in family E-7 x 578. Orthogonal comparisons of the F_2 progenies were planned on the basis of separating them into half-sib groups and using differences in midparent values as indicated by the Least Significant Bounds presented in Table 14.

The parental and midparental means for height along with the Least Significant Bound for midparent values appear in Table 15. The shorter parent differed at the .05 probability level from the taller parent in 2, 2, 2, and 4 of the 6 matings in the families 533 x 578, 540 x 578, 567 x 578, and E-7 x 578, respectively. Planned comparisons were made as

Table 13. Analysis of variance and orthogonal comparisons of height means of F_2 families

Source of variation		Mean height of comparisons in inches		D.F.	Height mean squares
Rows					2.16
Columns					.69
Families					154.59**
Comparison of families					
	533, 540 and 567 vs. E-7	13.1	14.6		87.66**
578	533 and 540 vs. 567	13.5	12.3		46.08**
	533 vs. 540	15.3	11.6		330.04**
Error					1.06

**Significant at the .01 probability level.

Table 14. Parental and midparental means for flowering time

Crosses	Flowering time mean of pod parent	Flowering time mean of pollen parent	Midparent mean flowering time	L.S.B.[a]
Family 533 x 578				
1 x 2	26.0	20.0*	23.0	21.3
3 x 4	26.7	22.2*	24.4	22.6
5 x 6	26.8	18.1*	22.5[b]	20.9
2 x 3	20.0*	26.7	23.4	21.7
4 x 5	22.2*	26.8	24.6	22.8
6 x 1	18.1*	26.0	22.0	-
Family 540 x 578				
1 x 2	28.7	23.4	26.4	23.2
3 x 4	16.1	18.4	17.3	-
5 x 6	20.7	22.5	21.6	18.5
2 x 3	23.4	16.1*	19.9	16.9
4 x 5	18.4	20.7	19.6	16.7
6 x 1	22.5*	28.7	25.8	22.6
Family 567 x 578				
1 x 2	21.0	18.0*	19.6	18.1
3 x 4	19.4	17.5	18.4	-
5 x 6	25.2	19.7*	22.4	20.8
2 x 3	18.0	19.4	18.6	17.2
4 x 5	17.5*	25.2	21.4	19.8
6 x 1	19.7	21.0	20.4	18.9
Family E-7 x 578				
1 x 2	34.4	24.0*	30.2	26.8
3 x 4	20.3*	35.6	27.7	24.5
5 x 6	22.1	19.8	21.0	-
2 x 3	24.0	20.3	22.4	19.4
4 x 5	35.6	22.1*	28.6	25.3
6 x 1	19.8*	34.4	28.0	24.7

[a]Least Significant Bounds calculated with standard errors from analyses of variance in Appendix Table 35.

[b]Less (earlier) than one or more of the underlined Least Significant Bounds in that half-sib group at the .05 probability level.

*Less (earlier) than the Least Significant Bound given in Table 5 for the later parent in the cross at the .05 probability level.

Table 15. Parental and midparental means for height of flowering stem

Crosses	Height mean of pod parent	Height mean of pollen parent	Midparent mean height	L.S.B.[a]
Family 533 x 578				
1 x 2	18.5	14.7	16.6	15.5
3 x 4	15.4	16.4	15.9	14.8
5 x 6	17.6	13.6*	15.6[b]	14.6
2 x 3	14.7	15.4	15.0	-
4 x 5	16.4	17.6	17.0	15.8
6 x 1	13.6*	18.5	16.1	15.0
Family 540 x 578				
1 x 2	9.9	9.4	9.6	-
3 x 4	10.5*	12.7	11.6	10.6
5 x 6	11.1	11.0	11.1	10.2
2 x 3	9.4	10.5	10.0	9.1
4 x 5	12.7	11.1*	11.9	10.9
6 x 1	11.0	9.9	10.4	9.5
Family 567 x 578				
1 x 2	13.4	10.2	11.8	11.0
3 x 4	10.0	11.6	10.8	10.0
5 x 6	12.4	8.2*	10.3	9.6
2 x 3	10.2	10.0	10.1	-
4 x 5	11.6	12.4	12.0	11.2
6 x 1	8.2*	13.4	10.8	10.0
Family E-7 x 578				
1 x 2	17.4	15.8	16.6	15.2
3 x 4	12.4*	18.9	15.7	14.4
5 x 6	14.2	13.3	13.8	-
2 x 3	15.8	12.4*	14.1	12.9
4 x 5	18.9	14.2*	16.6	15.2
6 x 1	13.3*	17.4	15.4	14.1

[a]Least Significant Bounds calculated with standard errors from analyses of variance in Appendix Table 35.

[b]Less (shorter) than one or more of the underlined Least Significant Bounds in that half-sib group at the .05 probability level.

*Less (shorter) than the Least Significant Bound given in Table 5 for the taller parent in the cross at the .05 probability level.

indicated previously.

The F_2 progeny means and deviations from midparent values for flowering time and height of flowering stem appear in Table 16. Within the 533 x 578 family there was an average, consistent deviation of 6.4 days toward lateness and of 0.7 inches toward taller plants. In the 567 x 578 family, there was an average, consistent deviation of 2.3 days toward lateness and of 1.3 inches toward taller plants. Deviations for flowering time and height were not consistent in the families 540 x 578 and E-7 x 578. However, in the E-7 x 578 family the inconsistency was small, with an average deviation of 1.6 days toward lateness and of 0.7 inches toward shorter plants. In the 540 x 578 family, the two deviations toward earliness are probably attributable to a clonal mean for F_1 sib-1 which is later than the true value as this parent had a coefficient of variation of 38.5 percent (Appendix Table 40). In comparable days, its mean was 11 days later in 1961 than its day of flowering in 1960. The correlation between the flowering times of the 24 F_1 plants in 1960 and the 24 F_1 clonal means in 1961 was +.568, which is different from zero at the .01 probability level. When the values for 540 x 578 F_1 sib-1 were omitted, the correlation coefficient was increased to +.672.

As shown in Appendix Table 36, which is a compilation of within family analyses, significant differences among F_2 progeny means were not obtained in all families. Partial analyses of variance and orthogonal comparisons of F_2 progeny means for flowering time appear in Table 17 for families 567 x 578 and E-7 x 578. In both of these families there were no significant differences between half-sib groups in mean flowering

Table 16. F_2 progeny means and deviations from midparent values for flowering time and height of flowering stem

F_1 sib-crosses	No. of F_2 plants	Flowering time in days after May 12, 1961			Height of flowering stem in inches		
		F_2 means	Deviation from midparent		F_2 means	Deviation from midparent	
			Earlier	Later		Shorter	Longer
Family 533 x 578							
1 x 2	127	28.6		5.6	14.8	1.8	
3 x 4	130	29.2		4.8	15.1	.8	
5 x 6	121	28.8		6.3	15.4	.2	
2 x 3	126	32.4		9.0	14.4	.6	
4 x 5	132	28.2		3.6	16.5	.5	
6 x 1	118	30.9		8.9	15.7	.4	
Family 540 x 578							
1 x 2	105	24.0	2.4		11.7		2.1
3 x 4	116	20.4		3.1	11.2	.4	
5 x 6	134	24.4		2.8	11.7		.6
2 x 3	129	21.2		1.3	11.6		1.6
4 x 5	129	22.2		2.6	11.9	-	
6 x 1	132	21.8	4.0		11.6		1.2

Table 16 (Continued).

F_1 sib-crosses	No. of F_2 plants	Flowering time in days after May 12, 1961			Height of flowering stem in inches		
		F_2 means	Deviation from midparent		F_2 means	Deviation from midparent	
			Earlier	Later		Shorter	Longer
Family 567 x 578							
1 x 2	133	20.6		1.0	13.2		1.4
3 x 4	133	20.3		1.9	11.2		.4
5 x 6	135	24.6		2.2	12.0		1.7
2 x 3	132	19.8		1.2	10.7		.6
4 x 5	130	27.5		6.1	13.7		1.7
6 x 1	137	21.6		1.2	12.8		2.0
Family E-7 x 578							
1 x 2	122	33.0		2.8	15.2	1.4	
3 x 4	126	28.9		1.2	14.2	1.5	
5 x 6	130	23.6		2.6	14.3		.5
2 x 3	130	24.9		2.5	13.1	1.0	
4 x 5	129	28.4	.2		16.3	.3	
6 x 1	106	28.8		.8	14.7	.7	

Table 17. Partial analyses of variance and orthogonal comparisons of F_2 progeny means for flowering time in families 567 x 578 and E-7 x 578

Source of variation	Flowering-time mean of comparisons in days after May 12, 1961		D.F.	Flowering-time mean squares
Progenies within family 567 x 578			5	73.13**
Between half-sib populations A and B	21.8	23.0	1	15.76
Progenies within A			2	45.22**
5 x 6 vs. 1 x 2 and 3 x 4	24.6	20.4	1	89.92**
1 x 2 vs. 3 x 4	20.6	20.3	1	.52
Progenies within B			2	129.71**
2 x 3 vs. 4 x 5 and 6 x 1	19.8	24.6	1	117.81**
4 x 5 vs. 6 x 1	27.5	21.6	1	141.61**
Error			15	4.31
Progenies within family E-7 x 578			5	87.46**
Between half-sib populations A and B	28.5	27.9	1	16.22
Progenies within A			2	173.82**
5 x 6 vs. 1 x 2 and 3 x 4	23.6	30.9	1	280.82**
1 x 2 vs. 3 x 4	33.0	29.0	1	66.83*
Progenies within B			2	36.72
2 x 3 vs. 4 x 5 and 6 x 1	24.9	28.4	1	72.77*
4 x 5 vs. 6 x 1	28.3	28.6	1	.68
Error			15	14.43

time, however, there were differences within three of the half-sib group at the .01 probability level.

Partial analyses of variance and orthogonal comparisons of F_2 progeny means for height in families 533 x 578, 567 x 578, and E-7 x 578 appear in Table 18. There were no significant differences between half-sib groups within families but there were differences for height at the .01 probability level in four of the six half-sib groups.

The F_2 progenies were analyzed on an individual plant basis. The removal of the variance due to replication differences from the total variance for each progeny estimates the F_2 variance which is V_{F_2} in the terms of Mather (1949). He designated the non-heritable variation of individuals as E_1, and obtained estimates of it by summing the variances of deviations of genetically homogeneous plants from the plot mean. In this study the estimate of the non-heritable variation of an individual, designated as E, was obtained by averaging over eight clones the summation of the variances of deviations of propagules from their respective clonal mean for the experiment. Thus, E is based on a similar number of plants as each F_2 progeny but does contain variance due to replication differences. Such a bias will tend to reduce the estimate of the genetic variation.

The F_2 variances, estimates of environmental variances, and genetic variances for flowering time and height in each F_2 progeny are presented in Table 19. The estimates of environmental variance associated with an individual plant ranged from 9 to 36 days for flowering time and from 4.3 to 4.6 inches for height. Within families 533 x 578 and 540 x 578, the

Table 18. Partial analyses of variance and orthogonal comparisons of F_2 progeny means for height in families 533 x 578, 567 x 578, and E-7 x 578

Source of variation	Height mean of comparisons in inches		D.F.	Height mean squares
Progenies within family 533 x 578			5	4.53
Between half-sib populations A and B	15.1	15.5	1	2.04
Progenies within A			2	.95
Progenies within B			2	9.34**
2 x 3 vs. 4 x 5 and 6 x 1	14.4	16.1	1	16.22**
4 x 5 vs. 6 x 1	16.4	15.8	1	2.48**
Error (Rows within plots)[a]			24	.76
Progenies within family 567 x 578			5	10.99**
Between half-sib populations A and B	12.1	12.4	1	.83
Progenies within A				8.04**
1 x 2 vs. 3 x 4 and 5 x 6	13.2	11.6	1	13.02**
3 x 4 vs. 5 x 6	11.2	12.1	1	3.06*
Progenies within B				
4 x 5 vs. 2 x 3 and 6 x 1	13.7	11.7	1	20.80**
2 x 3 vs. 6 x 1	10.7	12.8	1	17.22**
Error			15	.47

[a]Substituted for replications x progenies error which was 0.21.

*Significant at the .05 probability level.

**Significant at the .01 probability level.

Table 18 (Continued).

Source of variation	Height mean of comparisons in inches		D.F.	Height mean squares
Progenies within family E-7 x 578			5	9.43**
Between half-sib populations A and B	14.6	14.7	1	.14
Progenies within A			2	2.70
5 x 6 vs. 1 x 2 and 3 x 4	14.3	14.7	1	.88
1 x 2 vs. 3 x 4	15.2	14.2	1	4.52*
Progenies within B				
2 x 3 vs. 4 x 5 and 6 x 1	13.0	15.5	1	31.04**
4 x 5 vs. 6 x 1	16.3	14.7	1	10.56**
Error			15	.79

Table 19. F_2, genetic, and estimates of environmental variances and covariances for flowering time and height of flowering stem in each F_2 progeny

	Flowering time in days			Height in inches			Flowering time with height		
	V_{F_2}	V_{F_2}-E	E^a	V_{F_2}	V_{F_2}-E	E^a	Cov_{F_2}	Cov_{F_2}-E	E^a
Family 533 x 578			15.1			4.6			2.3
1 x 2	56.5	41.4		8.4	3.8		9.6	7.3	
3 x 4	57.6	42.6		6.6	2.0		2.6	.3	
5 x 6	51.1	36.0		5.6	1.0		7.7	5.4	
2 x 3	80.8	65.7		5.1	.5		5.8	3.5	
4 x 5	37.7	22.6		5.6	1.0		5.3	3.0	
6 x 1	101.2	86.1		6.1	1.5		10.7	8.4	
Family 540 x 578			36.2			4.5			-2.0
1 x 2	82.3	46.1		7.6	3.1		4.7	6.7	
3 x 4	58.6	22.4		4.5	.0		5.2	7.2	
5 x 6	52.4	16.2		5.9	1.4		5.3	7.3	
2 x 3	54.4	18.2		5.8	1.3		6.3	8.3	
4 x 5	44.7	8.5		6.4	1.9		4.4	6.4	
6 x 1	59.7	23.5		5.1	.6		4.0	6.0	

[a]Estimated from analyses in Appendix Table 38.

Table 19 (Continued).

	Flowering time in days			Height in inches			Flowering time with height		
	V_{F_2}	V_{F_2}-E	E	V_{F_2}	V_{F_2}-E	E	Cov_{F_2}	Cov_{F_2}-E	E
Family 567 x 578			8.6			4.3			-1.5
1 x 2	17.1	8.5		6.1	1.8		2.2	3.7	
3 x 4	35.5	26.9		5.0	.7		2.7	4.2	
5 x 6	36.2	27.6		4.2	.0		2.0	3.5	
2 x 3	16.2	7.6		6.0	1.7		.8	2.3	
4 x 5	77.0	68.4		5.7	1.4		7.4	8.9	
6 x 1	38.1	29.5		5.6	1.3		1.9	3.4	
Family E-7 x 578			14.1			4.6			- .2
1 x 2	60.4	46.3		7.7	2.4		.1	.3	
3 x 4	75.9	61.8		4.9	.3		5.2	5.4	
5 x 6	56.0	41.9		5.1	.5		2.5	2.7	
2 x 3	44.3	30.2		6.4	1.8		- .5	- .3	
4 x 5	74.6	60.5		6.0	1.4		5.5	5.7	
6 x 1	58.4	44.3		5.4	.8		1.9	2.1	

highest amount of genetic variance was 86 and 46, respectively.

In family 567 x 578 the greatest amount of genetic variance was 68, in the progeny from 4 x 5. This progeny was later at the .01 probability level than 6 x 1 in the comparison in Table 17. Within family E-7 x 578, the 3 x 4 and 4 x 5 progenies had genetic variances of 62 and 60, respectively. In Table 17, 3 x 4 was earlier than 1 x 2 at the .05 probability level and 4 x 5 was not different from 6 x 1.

The genetic variance for height is small in each of the F_2 progenies, however the environmental estimates are quite consistent from family to family.

The F_2 covariances, estimates of environmental covariances, and genetic covariances for flowering time and height are listed in Table 19. Designations analogous to those for variances were used. The estimates of environmental covariance ranged from -2.0 to +2.3. Except for one progeny the F_2 and genetic covariances were positive; the latter ranged from -0.3 to +8.9.

Heritability Estimates and Genetic Advance

Heritabilities for flowering time and height of flowering stem were computed between and within F_2 progenies. The former case was on a plot basis in which variance components for genetic effects and environmental effects were isolated from the analyses of variance in Appendix Table 36 using the following method:

Environmental variance, σ^2_e = the error mean square minus the rows-within-plots mean square.

Genetic variance, σ^2_g = the progenies mean square minus the error

mean square, followed with division by 4 replications.

The heritability values were computed as the ratio of $\frac{\sigma_g^2}{\sigma_g^2 + \sigma_e^2}$, which is the ratio of the genetic variance to the observed variance.

As pointed out by Burton (1952) the genetic variance can include the additive genetic variance, the variance due to dominance deviations from the additive scheme, the variance due to non-allelic gene interactions and the variance due to genotype-environment interactions. In order to obtain estimates of the additive portion of the genetic variance, heritabilities were computed by midparent-progeny regression. Within those families in which there was significant variation among F_2 progeny means, progeny plot values were paired with their respective midparent values obtained in that same replicate. The regression values obtained from the midparent-progeny covariance analysis are directly expressible as heritability percentages.

Heritability estimates of the genetic variation and the additive portion of the genetic variation are presented in Table 20. The genetic variation among F_2 progeny means ranges from 49 to 95 percent for flowering time, and from 26 to 97 percent for height. The estimates of the additive portion of the genetic variance must be interpreted with caution, for although the fit to linear regression was significant at the .01 probability level in each case, deviations from regression were significant at the .01 probability level in each case except for flowering time in family E-7 x 578. In this family the data indicate that 84 percent of the genetic variation for flowering time is additive.

There are several factors which may be inflating the regression

Table 20. Estimates of heritability based on variance components and midparent-progeny regression from analyses of F_2 families

	$\frac{\sigma_g^2}{\sigma_g^2 + \sigma_e^2}$		Midparent-progeny regression	
	Flowering time	Height	Flowering time	Height
Family 533 x 578				
Progenies within half-sib groups A and B	-[a]	.265	-[a]	.687
Progenies within group A		-[a]		
Progenies within group B		.585		
Family 567 x 578				
Progenies within half-sib group A and B	.870	.926	1.581	1.255
Progenies within group A	.868	.936		
Progenies within group B	.953	.973		
Family E-7 x 578				
Progenies within half-sib groups A and B	.489	.731	.838	.706
Progenies within group A	.770	-[a]		
Progenies within group B	-[a]	.909		

[a]No significant differences in progeny means.

values. Comstock and Robinson (1952) stated that the genotypic covariance between half-sib families and parent clones contains a confounded genotype-environment interaction variance when the clones and progenies are grown at the same time and location. The regression estimates in Table 20 were reduced when the error mean product and the midparent mean square were added to the numerator and denominator, respectively, in obtaining the ratio. There was a change from 1.581, .838, .687, 1.255, and .706 to 1.178, .757, .572, .929 and .633, respectively.

Panse and Bokil (1948) stated that regression overestimates the additive portion in the presence of dominance. Hoover (1952) postulated that the utilization of plot scores instead of individual plant scores should eliminate many of the dominance and epistatic effects. If the deviations of flowering-time means from midparent values presented in Table 16 are an indication of dominance, there is considerable dominance for lateness in the F_2.

Another factor which may be inflating the regression values is the difference in tetrasomic and disomic covariances. Kempthorne (1955) has determined the parent-offspring covariance in a random mating, autotetraploid population to be equal to one-half of the additive variance and one-sixth of the dominance variance. Whereas the parent-progeny covariance for diploids, as shown by Falconer (1961), is equal to one-half of the additive variance. Thus, with tetrasomic inheritance, fluctuations in the magnitude of the additive and dominance variances could influence the regression values. For example, if the dominance variance were three times that of the additive portion, then the covariance would be made up

of one-half additive and one-half dominance variances.

F_2 progeny heritabilities for flowering time and height were computed from the F_2, environmental, and genetic variances and covariances that appear in Table 19. The heritability values as obtained and presented in Table 21 are applicable only to individuals within the respective progenies from which the estimates were obtained. The genetic variation ranged for flowering time from 19 to 89 percent and for height from 0 to 45 percent. The genetic covariation for flowering time and height ranged from -55 to +96 percent. Selection for height appears to be more promising on an F_2 progeny or family mean basis, than on an individual plant basis, except for selection of later flowering plants with longer stems at time of flowering.

In utilizing heritability values as an aid to selection, the variability of the material from which selections are to be made should be considered. A high heritability coupled with a large amount of variability appears to offer the greatest opportunity for advance. The observed variability for flowering time in each of the F_2 progenies is presented as a percentage frequency distribution in Table 22. The magnitude of the genetic variability in each F_2 progeny is expressed as a genetic coefficient of variation and included in this table.

Selection for flowering time might be considered as follows. The additive portion of the genetic variance was estimated to be 83.8 percent in family E-7 x 578. The progeny 4 x 5 in this family has a heritability estimate of 81.2 percent. This progeny also has the least amount of deviation from the midparent value for flowering time and height, and has

Table 21. Estimates of heritability obtained from F_2 progeny variances, V_{F_2}, and covariances, Cov_{F_2}, and from environmental estimates, E, for flowering time and height

	Heritability in percent		
	$\frac{V_{F_2} - E}{V_{F_2}}$		$\frac{Cov_{F_2} - (+E)}{Cov_{F_2}}$ or $\frac{Cov_{F_2}}{Cov_{F_2} - (-E)}$
	Flowering time	Height	Flowering time with height
Family 533 x 578			
1 x 2	73.3	45.2	76.4
3 x 4	73.9	29.9	11.0
5 x 6	70.5	17.6	70.5
2 x 3	81.4	10.5	60.9
4 x 5	60.1	17.7	56.9
6 x 1	85.1	24.5	78.9
Family 540 x 578			
1 x 2	56.0	41.2	69.7
3 x 4	38.3	0.0	71.7
5 x 6	31.0	24.2	72.3
2 x 3	33.5	22.6	75.5
4 x 5	19.0	30.4	68.2
6 x 1	39.4	12.2	66.4

Table 21 (Continued).

	Heritability in percent		
	$\frac{V_{F_2} - E}{V_{F_2}}$	$\frac{Cov_{F_2} - (+E)}{Cov_{F_2}}$ or $\frac{Cov_{F_2}}{Cov_{F_2 - (-E)}}$	
	Flowering time	Height	Flowering time with height
Family 567 x 578			
1 x 2	49.4	29.9	58.4
3 x 4	75.7	14.5	63.6
5 x 6	76.1	0.0	56.0
2 x 3	46.5	28.6	34.5
4 x 5	88.8	24.6	82.7
6 x 1	77.4	23.4	54.6
Family E-7 x 578			
1 x 2	76.7	40.6	34.8
3 x 4	81.5	6.5	95.7
5 x 6	74.9	10.2	91.6
2 x 3	68.2	28.3	-55.3
4 x 5	81.2	24.1	96.0
6 x 1	75.9	15.2	89.3

Table 22. Observed variability for flowering time within F_2 progenies in terms of percentage frequency distributions, and genetic variability expressed as genetic coefficients of variation

	No. of plants	Percentage F_2 plants with first bloom in weeks after May 12, 1961								Genetic C.V.
		2	3	4	5	6	7	8	9	
Family 533 x 578										
1 x 2	127	-	18.9	32.3	29.1	11.8	7.9	-	0.8	22.5
3 x 4	131	-	14.5	31.3	35.9	9.9	6.9	0.8	-	22.3
5 x 6	121	-	17.4	33.9	33.0	7.4	5.8	2.5	0.3	20.8
2 x 3	126	-	13.5	21.4	32.5	15.9	11.9	4.0	0.8	25.0
4 x 5	131	-	13.0	38.2	41.2	3.0	3.0	1.5	-	16.9
6 x 1	117	-	23.9	18.8	25.6	17.9	6.8	6.0	0.8	30.0
Family 540 x 567										
1 x 2	106	0.9	72.6	9.4	3.8	3.8	4.7	2.8	1.9	28.3
3 x 4	116	7.8	69.8	12.9	1.7	3.4	3.4	0.9	-	23.2
5 x 6	134	2.8	46.3	30.6	13.4	6.0	3.0	0.7	-	16.5
2 x 3	129	-	80.6	12.4	0.8	1.6	3.1	0.8	0.8	20.1
4 x 5	129	0.8	58.1	27.9	8.5	0.8	1.6	2.3	-	13.1
6 x 1	132	2.3	68.2	15.2	6.1	5.3	1.5	-	1.5	22.2

Table 22 (Continued).

	No. of plants	Percentage F_2 plants with first bloom in weeks after May 12, 1961								Genetic C.V.
		2	3	4	5	6	7	8	9	
Family 567 x 578										
1 x 2	134	1.5	59.7	32.8	4.5	0.7	0.7	-	-	14.1
3 x 4	133	3.0	76.7	13.5	2.2	0.8	3.0	0.8	-	25.5
5 x 6	135	1.5	30.4	45.9	14.8	5.9	0.7	0.7	-	21.3
2 x 3	133	4.5	69.9	19.5	4.5	0.8	0.8	-	-	13.8
4 x 5	129	0.8	27.1	35.6	13.2	11.6	10.8	0.8	-	30.1
6 x 1	135	1.5	57.0	31.8	5.2	2.2	1.5	0.7	-	25.1
Family E-7 x 578										
1 x 2	122	-	4.1	34.4	31.1	9.8	15.6	4.1	0.8	20.6
3 x 4	126	-	27.0	28.6	21.4	11.9	7.9	2.4	0.8	27.2
5 x 6	130	0.8	53.1	26.9	10.0	6.2	2.3	-	0.8	27.4
2 x 3	130	-	36.2	41.5	13.8	4.6	3.8	-	-	22.1
4 x 5	129	-	21.7	40.3	18.6	9.3	7.0	1.6	1.6	27.4
6 x 1	106	-	25.5	35.8	19.8	9.4	5.7	3.8	-	23.1

a good distribution of variability.

Expected genetic advance was computed from the formula, $G_s = (k)(\sigma_A)(H)$, given by Allard (1960). In the formula, k is the selection differential in terms of standard units as obtained from Lush (1945, Table 12). The value, σ_A, is the phenotypic standard deviation obtained as the square root of V_{F_2}. The value, H, is the heritability estimate obtained as a product of the percentage estimates of the additive variance and the genetic variance.

If the four earliest-flowering plants (3 percent of the population) were selected, the expected genetic advance would be as follows:

$$2.26\ (8.64)\ (.812)\ (.838) = 13.3 \text{ days.}$$

The expected genetic advance does not make allowance for the fact that flowering time is a threshold character, thus such estimates of advance should be treated conservatively. The mean of this F_2 progeny was 28.4 days after May 12; hence the mean of the progenies from the four selections is expected to be 28.4 - 13.2 = 15.2 days after May 12, 1961. However, selection for maturity types intermediate to Viking and Empire appears to be more desirable than selection for types earlier than Viking or later than Empire. For in reality, selection for earliness, even if achievable, would not be profitable unless a better combination of characters resulted, for instance, greater vegetative growth but as early-flowering as Viking. The relationship between flowering time and the height of the flowering stem is considered in the next section.

Correlation Analysis

Correlation is a two-way average relationship between two variables, such as flowering time and height, that are consequences of common elements. The ease with which two quantitative characters may be combined or recombined is indicated by the relationship of the characters through inheritance. Genetic correlation coefficients estimate the degree of heritable relationship between two characters in a population.

Path coefficient analysis was considered by Peacock and Wilsie (1960) as being a useful method of studying genetic and environmental relationships. With random assignment of entries under the conditions of a field design, it may be assumed that there is no genotype-environment correlation, and the observed variance or covariance can then be partitioned into the environmental and genetic components. This analysis follows from Wright (1921) who stated that in considering two independent causal factors, each path coefficient, squared, will give a measure of the degree of determination of that factor and the sum of the two will equal unity. He considered a path coefficient as differing from a correlation coefficient in that the former has direction.

A path analysis diagram, as used by a number of researchers, appears in Figure 1. The path coefficient and correlation diagram symbols and the derivation of their estimates in terms of variance and covariance are given in Table 23. The generalized, expected mean squares for x and for y in analyses of variance are given in Table 24, along with the analogous expectations of mean products in the analysis of covariance.

The mean squares and products, and variance and covariance components

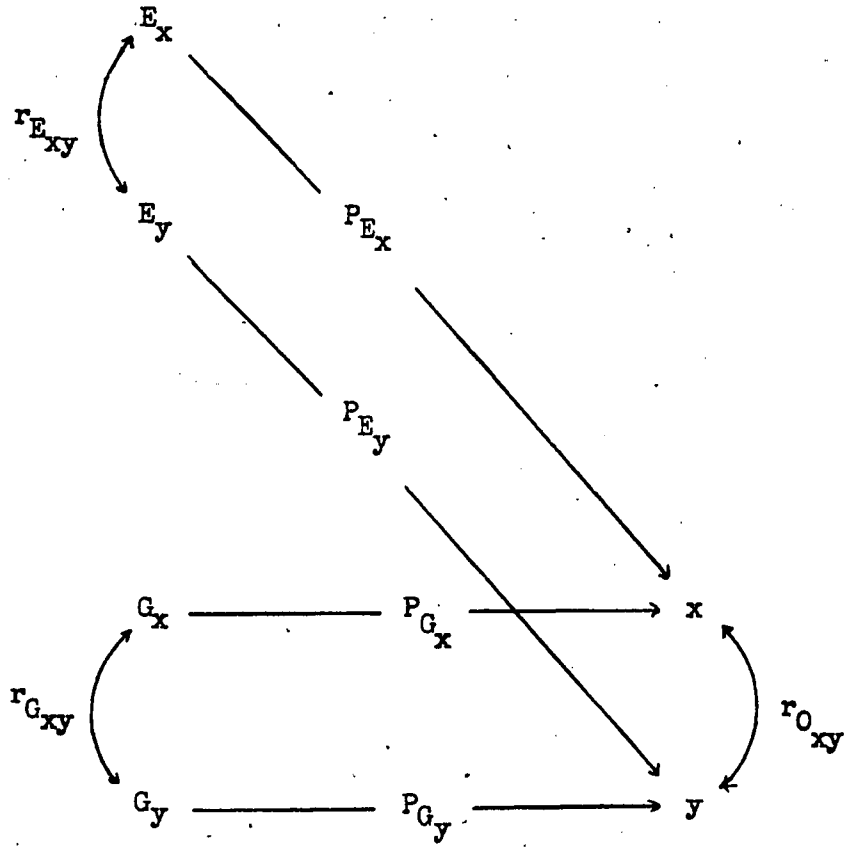

Figure 1. Path coefficient and correlation diagram.[a]

[a]Symbols are defined in Table 23.

Table 23. Path and correlation symbols with the derivation of their estimates from variance and covariance analyses

	Path coefficient diagram symbol	Derivation of estimates of path coefficient diagram symbols in terms of variance and covariance
Environmental correlation of x and y	$r_{E_{xy}}$	Error mean product for x and y, divided by the geometric mean of the error mean squares for x and y
Genetic correlation of x and y	$r_{G_{xy}}$	Covariance component for x and y, divided by the geometric mean of the variance components for x and y
Observed correlation of x and y	$r_{O_{xy}}$	Entries mean product for x and y, divided by the geometric mean of the entries mean squares for x and y
Environmental path coefficient for x	P_{E_x}	Square root of the error mean square for x, divided by the square root of the entries mean square for x
Genetic path coefficient for x	P_{G_x}	Square root of the remainder from subtracting the error mean square for x from the progenies mean square for x, followed with division by the square root of the progenies mean square for x
Environmental path coefficient for y	P_{E_y}	Same as for x, using values for y
Genetic path coefficient for x	P_{G_y}	Same as for x, using values for y

Table 24. Entries and error expected mean squares in the analyses of variance of x and y, and expected mean products in the analysis of covariance of x and y

	Expected mean squares for x	Expected mean products for x and y	Expected mean squares for y
Entries	$\sigma^2_{e_{xx}} + n \quad \sigma^2_{g_{xx}}$	$\sigma_{e_{xy}} + n \quad \sigma_{g_{xy}}$	$\sigma^2_{e_{yy}} + n \quad \sigma^2_{g_{yy}}$
Error	$\sigma^2_{e_{xx}}$	$\sigma_{e_{xy}}$	$\sigma^2_{e_{yy}}$

used in the correlation and path coefficient analyses of flowering time and height are presented in Tables 37, 38, and 39 of the Appendix. The computational difficulties as discussed by Peacock and Wilsie (1960), in general, did not occur in these analyses. The relationships within flowering time and within height are considered first, and then the relationship of flowering time with height is considered.

The path and correlation coefficients for parent-offspring relationships within flowering time and within height appear in Table 25. The observed correlations are relatively high with three of the four being different from zero at the .05 probability level. The genetic correlations were higher than the observed correlations indicating that the environment was affecting the parent-progeny genetic relationship. The environmental correlation values were negative in the family 567 x 578 and positive in the family E-7 x 578 indicating a differential effect of the environment. The genetic path coefficients were from two to four times greater than the environmental path coefficients indicating that genetic effects contributed more to parent-offspring relationships than environmental effects. The squares of the path coefficients indicated that from 84 to 96 percent of the relationship was the result of genetic causes.

The coefficients expressing the relationship between flowering time of the F_1 midparent and height of the F_2 means appear in Table 26. The observed correlations were non-significant in contrast to those in Table 25 in which 3 out of 4 were significant, with 4 degrees of freedom in each case. However, when the progenies of the two families were pooled, an observed correlation of +.821 was obtained, which is significant at the .01 probability level and 10 degrees of freedom.

Table 25. Environmental, genetic and observed correlations, and environmental and genetic path coefficients for parent-offspring relationships involving the characters flowering time and height of flowering stem

	Path coefficient diagram symbol[a]	F_1 midparents (x) and F_2 means (y) 567 x 578		E-7 x 578	
		Flowering time	Height	Flowering time	Height
Environmental correlation	$r_{E_{xy}}$	-.189	-.110	.297	.526
Genetic correlation	$r_{G_{xy}}$	.904	.916	1.032[b]	.817
Observed correlation	$r_{O_{xy}}$	.822*	.835*	.941**	.782
Environmental path coefficient for F_1 midparents	P_{E_x}	.302 (.091)[c]	.325 (.106)	.273 (.074)	.343 (.118)
Genetic path coefficient for F_1 midparents	P_{G_x}	.955 (.912)	.948 (.899)	.962 (.925)	.937 (.878)
Environmental path coefficients for F_2 means	P_{E_y}	.243 (.059)	.211 (.044)	.406 (.165)	.307 (.094)
Genetic path coefficients for F_2 means	P_{G_y}	.970 (.941)	.978 (.956)	.916 (.839)	.953 (.908)

[a]Estimates computed from Appendix Table 37.

[b]True correlation assumed to be near unity.

[c]Square of the path coefficient.

*Significant at the .05 probability level (4 D.F.).

**Significant at the .01 probability level (4 D.F.).

Table 26. Environmental, genetic and observed correlations for flowering time of the F_1 midparents and height at flowering time of the F_2 means

	Path coefficient diagram symbol[a]	F_1 midparents for flowering-time (x) and F_2 means for height (y)	
		567 x 578	E-7 x 578
Environmental correlation	$r_{E_{xy}}$	.026	-.244
Genetic correlation	$r_{G_{xy}}$	.606	.760
Observed correlation	$r_{O_{xy}}$	.566	.675

[a]The respective genetic and environmental path coefficients can be obtained from Table 26 for F_1 midparent flowering time and F_2 means of height at flowering time.

Further analyses were made to determine the relationship of height and flowering time. The coefficients from analyses of propagules of parental clones are presented in Table 27. Two of the four environmental correlations were significant at the .01 probability level, with one being positive and one being negative. The observed correlation for family E-7 x 578 was positive and significant at the .01 probability level.

The coefficients from analyses of individual plants within progenies appear in Table 28. The "within-progenies" estimates contain both genetic and environmental effects, and are averages of phenotypic correlations given for each progeny in Table 29. All four of the within-progenies correlations were positive and significant at the .01 probability level. Within family 533 x 578, both the observed and the genetic correlations were negative. Selection of one of the earliest flowering F_2 progenies in this family could result in the selection of one of the tallest F_2 progenies.

In all cases, the genetic correlations were larger than and had the same sign as the observed correlations. Three of the four environmental path coefficients for flowering time in the clonal analysis (Table 27) were smaller than the within-progenies path coefficients (Table 28). The one exception was in family E-7 x 578, in which 13.6 percent of the relationship was attributable to environment versus 5.1 percent attributable to environment plus genetic differences among full-sib plants. There was a similar comparison of 10.0 versus 3.2 percent for height in family 567 x 578.

Environmental, genetic, and observed correlations between flowering time and height of flowering stem for each F_2 progeny appear in Table 29.

Table 27. Environmental, genetic and observed correlations, and environmental and genetic path coefficients for flowering time and height of flowering stem from clonal analyses

	Path coefficient diagram symbol[a]	Flowering time (x) and height at flowering time (y)			
		533 x 578	540 x 578	567 x 578	E-7 x 578
Environmental correlation	$r_{E_{xy}}$	.271**	-.160	-.253**	-.015
Genetic correlation	$r_{G_{xy}}$	.622	.505	.178	.924
Observed correlation	$r_{O_{xy}}$	.612	.450	.159	.905##
Environmental path coefficient for flowering time	P_{E_x}	.147 (.022)[b]	.204 (.042)	.105 (.011)	.368 (.136)
Genetic path coefficient for flowering time	P_{G_x}	.988 (.978)	.979 (.958)	.995 (.990)	.929 (.863)
Environmental path coefficient for height	P_{E_y}	.176 (.031)	.360 (.130)	.316 (.100)	.156 (.024)
Genetic path coefficient for height	P_{G_y}	.984 (.969)	.933 (.870)	.948 (.899)	.988 (.976)

[a]Estimates computed from Appendix Table 38.

[b]Square of path coefficient.

**Significant at the .01 probability level (n-2 D.F.)

##Significant at the .01 probability level (6 D.F.)

Table 28. Environmental, genetic and observed correlations, and environmental and genetic path coefficients for flowering time and height of flowering stem from individual plant analysis of F_2 progenies

	Path coefficient diagram symbol[a]	Flowering time (x) and height at flowering time (y)			
		533 x 578	540 x 578	567 x 578	E-7 x 578
Within progenies correlation	$r_{E_{xy}}$	.338**	.274**	.194**	.101**
Genetic correlation	$r_{G_{xy}}$	-.528	-	.646	.574
Observed correlation	$r_{O_{xy}}$	-.492	.683	.630	.552
Within progenies path coefficient for flowering time	P_{E_x}	.460 (.212)[b]	.476 (.226)	.178 (.032)	.225 (.051)
Genetic path coefficient for flowering time	P_{G_x}	.888 (.788)	.880 (.774)	.984 (.968)	.974 (.949)
Within progenies path coefficient for height	P_{E_y}	.295 (.088)	-	.177 (.032)	.201 (.040)
Genetic path coefficient for height	P_{G_y}	.955 (.912)	-	.984 (.968)	.980 (.960)

[a]Estimates computed from Appendix Table 39.

[b]Square of the path coefficient.

**Significant at the .01 probability level.

Table 29. Environmental, genetic and observed correlations between flowering time and height of flowering stem from individual plant analyses within each F_2 progeny

	Environmental correlation[a] $r_{E_{xy}}$	Genetic correlation $r_{G_{xy}}$	Observed correlation[b] $r_{O_{xy}}$
Family 533 x 578			
1 x 2	-.500	.584	.440**
3 x 4	.895	.031	.130
5 x 6	-.333	.911	.454**
2 x 3	.334	.592	.284**
4 x 5	-.142	.627	.361**
6 x 1	-.458	.745	.431**
Family 540 x 578			
1 x 2	.899	.268	.187
3 x 4	.559	.444	.318**
5 x 6	.647	.417	.301**
2 x 3	.605	.468	.354**
4 x 5	.745	.378	.258**
6 x 1	.892	.347	.231**

[a]Due to replication effects (2 D.F.).

[b]Due to individual plant effects (n-2 D.F.).

**Significant at the .01 probability level.

Table 29 (Continued).

	Environmental correlation $r_{E_{xy}}$	Genetic correlation $r_{G_{xy}}$	Observed correlation $r_{O_{xy}}$
Family 567 x 578			
1 x 2	-.200	.362	.211*
3 x 4	.150	.317	.201*
5 x 6	.212	.286	.160
2 x 3	-.590	.238	.082
4 x 5	-.350	.425	.352**
6 x 1	.749	.232	.126
Family E-7 x 578			
1 x 2	-.969*	.016	.006
3 x 4	-.756	.279	.267**
5 x 6	.252	.163	.149
2 x 3	-.484	-.045	-.031
4 x 5	-.070	.268	.257**
6 x 1	-.985*	.121	.108

*Significant at the .05 probability level.

The environmental correlations were computed from variances and covariances for replication differences. The observed correlations were computed from Cov_{F_2} and V_{F_2} in Table 19. The genetic correlations were computed from the genetic covariances and genetic variances in the same table, except for the substitution of V_{F_2} for genetic variance in those cases in which there was a positive genetic covariance and a negative E.

The environmental correlations ranged from -.985 to +.899, and there were two which were significant at the .05 probability level. These were in family E-7 x 578 and involved F_1 sib-1, the progeny of which showed considerable iron chlorosis in certain replications. Of the 24 observed correlations, 13 were significant at the .01 probability level.

The genetic correlations were larger than the observed correlations except for the 1 x 2 progeny of 533 x 578. The genetic correlations were positive except for the 2 x 3 progeny of family E-7 x 578. In this case the genetic, observed, and environmental correlations were -.045, -.031, and -.484, respectively. The observed and environmental correlations were non-significant. The negative genetic correlation could be due to chance but it does suggest that the plants within this progeny should be observed further.

Experimental Precision and Efficiency

Precision, according to Cochran and Cox (1957), is the repeatability of measurements and accuracy is the closeness with which a measurement approaches the true value. A comparison of the precision of two designs, termed relative efficiency, can be obtained from the inverse ratio of the

error variances per unit.

The relative efficiency of a Latin square design compared to a randomized block design for flowering time and height of flowering stem are presented in Table 30. The Latin square was more efficient than a grouping of rows in the case of flowering time but less efficient in the case of height of flowering stem. Conversely, the Latin square was about as efficient as a grouping of columns for flowering time but more efficient for height of flowering stem. It should be noted that observations were made by column groupings. There was a correlation between the ratios of replication variance to total variance for the 24 F_2 progenies and the F_2 progeny means of +.708, which is different from zero at the .01 probability level. That is, there was a relationship between later flowering time means and greater replication variance apparently as a result of observational and environmental error increasing with time.

In the main experiment, the seedling progenies were F_2 populations and thus were considered to be highly heterogeneous. Once the decision was made to sample from 100 to 150 plants from each F_2 population it was necessary to decide how many plants were needed per plot so that the genetic variability of the material from replication to replication did not contribute greatly to the error variance. The best compromise appeared to be a sample size of 32 plants per plot with four replications. The plots were set up with 2 rows of 16 plants per row and by means of sub-sampling methods described by Snedecor (1956) a within-plots component of variance was estimated by analyzing the two-row plots on a row

Table 30. Relative efficiency of the 4 x 4 Latin square design in comparison to a randomized block design of 4 replications of 4 families

	Relative efficiency of the Latin square compared to a randomized block design, in percent	
	Rows grouping	Columns grouping
Flowering time		
Clonal experiment	178.6	109.4
F_2 progenies	244.5	100.7
Height of flowering stem		
Clonal experiment	87.3	130.4
F_2 progenies	98.0	135.4

basis (Appendix Table 36). The predicted error variances for experiments with eight replications of one-row plots were computed. The relative efficiencies of the proposed experiments in comparison to those with four replications of two-row plots are presented in Table 31. The utilization of twice as many replications and half as many plants per plot would have resulted in an increase in efficiency ranging from 0 to 70 percent for the characters studied.

Whether or not the sample sizes used were sufficient to achieve a desired level of precision in estimating population parameters may be determined by a method given by Graybill and Kneebone (1959). A confidence interval less than a certain percentage of the general source

Table 31. Relative efficiency of 8 replications with 16 F_2 plants per plot in comparison to 4 replications with 32 F_2 plants per plot as determined from half-plot analysis

	Relative efficiency in percent	
	Flowering time	Height at flowering time
F_2 progenies		
533 x 578	147.8	-[a]
540 x 578	143.8	100.0
567 x 578	122.0	117.3
E-7 x 578	170.1	146.2

[a]See Appendix Table 36.

mean is specified. The coefficient of variation typical for a given character of a given species is divided by this percentage value. Sample size numbers are read off a chart at probabilities that the values obtained will be within the range set.

The average coefficients of variation for flowering time and for height of flowering stem are given in Table 32 for the F_2 progeny families observed in 1961. Also included in this table are the average progeny sizes used and the sample sizes needed under the conditions of 95 percent probability, an average length of the confidence interval less than 10 percent of the source mean, and the respective coefficients of variation. A sample size of approximately 135 and 55 plants was necessary for studying flowering time and height, respectively, in F_2 material

Table 32. Average progeny size used in F_2 families and the sample size needed to have a 95 percent probability and to obtain a confidence interval less than 10 percent of the source mean, with the respective coefficients of variation for flowering time and height of flowering stem

Family	Average number of plants per progeny	Flowering time C.V. in %	Necessary number of plants per progeny	Height of flowering stem C.V. in %	Necessary number of plants per progeny
533 x 578	126	26.5	115	16.3	40
540 x 578	124	34.2	140	20.7	65
567 x 578	133	25.8	105	19.1	60
E-7 x 578	124	28.2	130	16.6	45
Over families	127	28.7	135	18.2	55

of birdsfoot trefoil. A sample size of 40 to 50 propagules was needed for obtaining flowering time and height values of parental material as indicated in Table 33.

Within two of the families, there were no significant differences among the flowering-time means of the F_2 progenies when analyzed on a plot basis. The fact that differences were not obtained is attributable in part to the fact that there were few differences among the midparent values. Another causal factor was the failure to obtain plants in the group of six random selections which were as late as the late parent.

The use of more crosses, say a diallel set of fifteen, would have increased the probability of different parental combinations but would have limited the number of families. The use of more selections would have increased the probability of having an array representing the F_1, but would have increased the amount of parental material to be studied. The better compromise would appear to have been the use of random paired crosses of twelve random selections from each F_1 which would have yielded 6 F_2 progenies in each family.

Table 33. Average sample size used per clone and the sample size needed to have a 95 percent probability and to obtain a confidence interval less than 10 percent of the source mean, with the respective coefficients of variation for flowering time and height of flowering stem

Family	Average number of propagules per clone	Flowering time C.V. in %	Necessary number of propagules per clone	Height of flowering stem C.V. in %	Necessary number of propagules per clone
533 x 578	17	13.9	30	14.2	35
540 x 578	16	20.7	65	20.8	65
567 x 578	16	13.4	30	19.4	60
E-7 x 578	16	14.3	35	14.1	35
Over families	16	15.6	40	17.1	50

DISCUSSION

The environment under which observations of flowering time were made, not only fluctuated but had a certain seasonal change in daylength and temperature. That is, those plants which flowered late were subjected to the same environment as early-flowering plants plus the environment that occurred in the interim. The daylength (sunrise to sunset) at 42° north latitude reaches 14 hours on April 29 and 15.2 hours on June 7. The daylength stays approximately at 15.2 hours until July 3 and then decreases to 14 hours on August 11, 13 hours on September 3, and 12 hours on September 25. Effective daylength may include up to 30 minutes before and after sunrise and sunset, respectively.

In the greenhouse during the winter of 1960 and 1961, the seven original parents did not flower under a daylength of 8 to 9 hours. Thus, all of the parents appeared to have a critical photoperiod above 8 or 9 hours, including the introduction from Switzerland. The days to first flower were determined for two propagules of each parent placed under 17 to 18 hour daylengths on December 31, 1960. The parents 578, 579, 2186, 533, 540, 567 and E-7 flowered in an average of 33, 32, 35, 43, 40, 32, and 33 days, respectively. There was no clear distinction between early and late-flowering parents for photoperiodic response in these data. Flowering of the Viking clones, 578 and 579, was similar to that of the Empire clone, E-7. Such was not the case for spring and fall flowering in the field.

At the end of the first season of establishment in the field, flowering was observed on October 5, 1960 in the E-7 x 578 family. Sixty

percent of the E-7 propagules and none of the 578 propagules were flowering. The percent of plants flowering ranged from 0 to 82 for the six F_1 sib-selections and from 4 to 22 for the six F_2 progenies. Only 3 plants were flowering in the other three families.

In the fall of 1961, observations were made on eight established propagules of 578 and E-7 which had flowered during the season. Within the Viking clone, one was flowering September 8, and none September 29. However, in the Empire clone, all were flowering September 8 and seven on September 29.

Clone E-7 flowers about 3 weeks later than 578 in the spring, indicating that the Empire clone has a greater photoperiodic requirement than the Viking clone. However, the fall flowering indicates that E-7 has less of a photoperiodic requirement. It is known that decreasing temperatures can reduce the critical photoperiod. The mature growth of E-7 apparently must be more subject to this effect than the growth of 578.

The appearance of the first flower on a plant is some indication that conditions became favorable for flowering from 3 to 4 weeks earlier. In the greenhouse during the spring of 1962, five late-flowering clones (F_2 selections from Empire x Viking which flowered about 5 weeks after May 12, 1960) flowered in 3 to 4 weeks after being placed under continuous light. Joffe (1958), under 16 and 18 hour daylengths, obtained the first normal flower in 23 days. Between the average time of flowering for 578 to that for E-7, there was an accumulation of 15,048 air temperature degree-hours and 362 hours of daylight in 24 days for 1960 and 12,240

degree-hours and 288 hours of daylight in 18 days for 1961. The effects of heredity, daylength, and temperature appear to be confounded.

Differences between Empire and Viking for flowering time and height are due undoubtedly to differences in gene frequencies. Within an autotetraploid individual, gene frequency at a locus may be either 0, .25, .50, .75 or 1. Following the reasoning of Mather (1949, p. 126), the fact that heterozygous parents had to be used in this study should not have been a limiting factor. The genetic differences between the early and late flowering parents should have been much greater than the genetic heterozygosity within parents. As it was desired to investigate genetic differences between early and later flowering plants, and not within groups of early or late plants, differences (heterozygosity) were regarded as extraneous sources of variation.

The heritable variation was separated from the non-heritable variation of the F_2 in this study. Except for midparent-progeny regression, the additive variance could not be partitioned from the total genetic variance. As discussed by Cooper (1959) most of the genetic variation in flowering-time studies seems to be additive.

The non-heritable variation within plots should be less than between plots. In this study estimates of the amount of environmental variation associated with an individual plant ranged (over families) from 8.6 to 36.2 days for flowering time and from 4.3 to 4.6 inches for height (length) of flowering stem. Cooper (1959) used clonal material and found in ryegrass (over 3 years) from 1.2 to 4.6 days error variance associated with a single plant. Over a period of 3 years, Mather and Vines (1952)

used homozygous lines and obtained estimates of E_1 which ranged from 4 to 12 days and 5 to 11 inches in Nicotiana rustica.

An estimate of environmental variance associated with a propagule undoubtedly is not equivalent to the environmental variance associated with an individual F_2 plant. Within each family of this study, the estimates were based upon 8 clonal genotypes, with one of the eight being common to each family. The fact that flowering-time estimates varied from family to family indicates that genotypes reacted differently to the environment. Thus, the genotypes of an F_2 population would have to be studied as clones in order to measure the genotype-environment (replication) interaction.

If F_2 genotypes responded differently to the environment in this study, the variance due to genotype-replication interaction is included in the estimates of genetic variance. However, the manner in which environmental estimates were computed resulted in the inclusion of interaction variance in them. The clone 578, which was included in each block of the experiment will serve to demonstrate this point. An estimate of E for flowering time based on deviations from the mean of 578 (over the experiment) would be 8.5 days. When deviations from plot means are used and the variances summed over 16 blocks, an average estimate of 6.3 days is obtained. However, the estimates of E based on the mean of clone 578 in each of four blocks varied from family to family. In families 533 x 578, 540 x 578, 567 x 578, and E-7 x 578 the estimates were 13.5, 5.0, 3.4, and 6.6 days, respectively.

Dominance of flowering time in progenies as measured by deviation

from midparent values is somewhat anomalous in this study. The F_1 progenies tended to show partial dominance for earliness of flowering and the F_2 progenies partial dominance for lateness of flowering. The F_1 progenies involving 578, 579 and 2186 were 8, 5 and 11 days earlier than the midparent, respectively. The F_1 progenies involving 533, 540, 567 and E-7 were 6, 10, 10 and 7 days earlier than the midparent, respectively.

Although six of the twelve F_1 progenies were varietal backcrosses to Viking, all of the crosses involved unrelated plants. There is the possibility of heterosis in the F_1 progenies. The data are somewhat limited, but they indicated that F_1 progenies, although earlier than the flowering-time midparent, were taller than the midparent for height of flowering stem. In a sample of seventeen E-7 x 578 F_1 plants (in 1961) there was a deviation of 8 days toward earliness and 1.5 inches toward longer flowering stems. There was a positive correlation between these two characters of .625 which is different from zero at the .01 probability level. Thus, increasing height was dependent upon later flowering in the progeny but not so in relation to the midparent values.

The F_1 progenies (in 1960) of 533 x 578, 540 x 578, 567 x 578 and E-7 x 578 were 4, 10, 9 and 9 days earlier than the midparent. The corresponding F_2 families (in 1961) were 0, 5, 7, and 1 days later than the midparents of 533, 540, 567 and E-7 with 578, respectively. On this basis there is a shift from partial dominance for earliness to no dominance in the families 533 x 578 and E-7 x 578 and to partial dominance for lateness in the families 540 x 578 and 567 x 578. It is entirely

possible with sufficient sampling and mating combinations that F_2 family means for flowering time can be expected to approach the original mid-parent value. As discussed previously, the earlier F_1 sib-parent differed significantly from the later parent in each of the matings in the 533 x 578 family, and the E-7 x 578 F_1 sib-selections were considered to be representative of the F_1 population.

Most of the F_2 progenies were later than their respective sib-midparent values. In the 533 x 578 family, all six of the progenies had means which were not only later than the midparent but were later than the range of the sib-parents.

In the E-7 x 578 family, five of the progenies had means that were later than the midparent values. Comparisons of the six F_1 sib-selections in backcrosses to 578 and E-7 can be made from data obtained in 1962. Five of the six backcrosses to 578 were later than the midparent from 0.8 to 4.6 days. In the backcrosses to E-7 there were also five which were later than the midparent from 2.3 to 4.5 days. However, when the twelve backcrosses, were pooled into one population, the weighted mean was 1 day earlier than the midparent of E-7 and 578. A sample of twelve F_1 plants deviated 6.5 days earlier than the midparent.

The degree and direction of dominance may be dependent upon the scale of the observations. Thus, the above comparisons of progeny means with midparent values may not present the real case. The comparisons with the grand-midparent values may be somewhat more valid in that they allow a generation of recombination. As pointed out by Falconer (1961) additive variance can arise from genes with any degree of dominance or

epistasis; hence, dominance as it has been considered here contributed little information about the nature of gene effects.

In the field the blocks containing the E-7 x 578 F_2 family were readily distinguishable (by the profuseness of flowering) from the blocks of 533 x 578, 540 x 578 and 567 x 578 F_2 families. Within these latter three families, especially in the 533 x 578 F_2 family, umbels with only one floret were observed quite frequently. These observations are in agreement with the F_1 data which indicated that progenies from E-7 would have the best seed production potential.

SUMMARY AND CONCLUSIONS

Flowering time was studied in clonal and segregating material of birdsfoot trefoil under field conditions. Parental and F_1 material was observed in 1960, and parents, sib-parents, F_1 and F_2 plants were observed in 1961.

The analysis of twelve F_1 progenies indicated that there were significant genetic differences among the early and among the late-flowering parents. There were no significant differences within progenies for first, second, and third umbels to flower. The mean of each progeny was earlier than the respective midparent value.

The analysis of the F_1 progenies indicated that the Swiss introduction had better combining ability for seed production than the Viking parents. The Empire clone had better combining ability for seed production than the other late-flowering parents which were Empire x Viking F_2 selections. There were also significant genetic differences among the parents for number of florets per umbel.

Observations indicated that late-flowering parents which were similar in flowering time were different in height of flowering stem. There were significant differences for height among clonal families and among sib-parents within families.

Additional samples of F_1 progenies observed in 1961 ranked in the same flowering-time order as in 1960 but were estimated to be a week later on the average. This estimate was found to agree with temperature summations. A correlation of +.568 (significant at the .01 probability level) was obtained between the 24 F_1 clonal means for flowering time in

1961 and the flowering time of the corresponding 24 F_1 plants in 1960.

The F_2 family means were from 1.4 to 6.6 days later than the F_1 family means. Two of the F_2 family means were the same as and two were later than the grand-midparent values. The parental and sib-parental material showed considerable environmental variation. The frequency distribution of the F_2 families differed. Estimates of early-flowering transgressive segregation ranged from 0.4 to 2.2 percent of the F_2 populations and from 2 to 4 days in extent. Similar estimates for late flowering ranged from 0.5 to 9.6 percent and from 5 to 17 days. Analyses indicated that there were significant differences among family means for flowering time and height of flowering stem.

Most of the F_2 progeny means were later than the respective sib-midparent value. Significant differences were detected among the F_2 progeny means on a plot basis for flowering time in two families and height in three families. Half-sib groups within these families did not differ significantly for flowering time or height.

Estimates of environmental variance associated with an individual plant ranged over families from 9 to 36 days for flowering time and from 4.3 to 4.6 inches for height. Environmental estimates of covariance ranged from -2.0 to +2.3.

Variance component analyses gave heritability estimates of genetic variation among F_2 progeny means that ranged from 49 to 95 percent for flowering time, and from 26 to 97 percent for height. Midparent-progeny regression indicated that 84 percent of the genetic variation for flowering time in one family was additive.

Heritability estimates were obtained for flowering time and height in each F_2 progeny. Estimates ranged from 19 to 89, 0 to 45, and -55 to +96 percent for flowering time, height, and flowering time with height, respectively. The low estimates for height indicated that selection on the basis of F_2 progeny means might be more successful than individual F_2 plant selection. The covariation estimates indicated that there was more basis for selecting later-flowering plants with longer flowering stems than taller, early-flowering plants.

The observed and genetic correlations for flowering time with height on a progeny mean basis were positive in three families and negative in the other family. Within the 24 F_2 families there were 23 positive observed correlations, thirteen of which were significant at the .01 probability level. Except for one case the genetic correlations were larger than the respective observed correlations.

It is concluded that genetic differences exist between families, progenies, and plants for flowering time and height of flowering stem and that there is generally an association within families and progenies of later flowering with longer flowering stems.

On the basis of the results obtained in this study, it appeared that 6 random paired crosses involving 12 F_1 plants would have been a more satisfactory method of obtaining F_2 progenies than chain crosses. However, this would have required studying twice as many F_1 sib-selections and a consideration of sample size indicated that approximately one-third as many propagules per clone were needed as F_2 plants per progeny. Although

a replication of F_2 plants is not a true replication, the results indicated also that an experiment with half as many plants per plot and twice as many replications would have been more efficient.

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APPENDIX

Table 34. Analyses of variance of clonal families for flowering time and height of flowering stem

	D.F.	Flowering time mean squares	Height mean squares
Within family 533 x 578			
Replications	3	15.21	1.80
Clones	7	167.63**	35.94**
Error	21	5.20	1.13
Within family 540 x 578			
Replications	3	8.03	8.28**
Clones	7	222.63**	7.26**
Error	21	17.38	.98
Within family 567 x 578			
Replications	3	12.02*	1.09
Clones	7	269.93**	10.06**
Error	21	2.62	1.12
Within family E-7 x 578			
Replications	3	80.98**	5.31
Clones	7	248.67**	46.90**
Error	20[a]	11.29	2.19

*Significant at the .05 probability level.

**Significant at the .01 probability level.

[a]Adjusted for missing plot.

Table 35. Analyses of variance of the flowering-time and height-of-flowering-stem midparent values involving the F_1 sib-parents in each of the four families studied

	D.F.	533 x 578	540 x 578	567 x 578	E-7 x 578
			Mean squares for flowering time		
Replications	3	12.14**	22.03**	9.16**	73.08**
Midparents	5	4.39*	53.49**	9.87**	55.42**
Error	15	1.15	3.70	.90	4.12
			Mean squares for height of flowering stem		
Replications	3	.49	6.31**	1.53**	2.04
Midparents	5	1.95*	3.34**	2.38**	5.70**
Error	15	.47	.34	.25	.67

*Significant at the .05 probability level.

**Significant at the .01 probability level.

Table 36. Compilation of within family analyses of variance of F_2 means for flowering time and height of flowering stem

	D.F.	Flowering time mean squares	Height mean squares
Replications within families			
533 x 578	3	108.86**	.43
540 x 578	3	21.61	1.51
567 x 578	3	8.29	1.07
E-7 x 578	3	108.97**	1.95
Progenies within families			
533 x 578	5	20.86	4.53**
540 x 578	5	20.13	.46
567 x 578	5	73.13**	10.99**
E-7 x 578	5	87.46**	9.43**
Error within families			
533 x 578	15	9.83	.21
540 x 578	15	13.65	.57
567 x 578	15	4.31	.47
E-7 x 578	15	14.43	.79
Rows within plots			
533 x 578	24	3.46	.76
540 x 578	24	5.27	.58
567 x 578	24	2.74	.34
E-7 x 578	24	2.54	.29

Table 37. Mean squares and products and variance and covariance components obtained from analyses of plot means

		F_1 midparents		F_1 midparents with F_2 progenies		F_2 progenies	
	D.F.	Mean squares	Variance components	Mean products	Covariance components	Mean squares	Variance components
567 x 578							
Flowering time							
Progenies	5	9.87**	2.24	15.61	3.97	36.52**	8.59
Error	15	.90		-.26		2.15	
Height							
Progenies	5	2.38**	.53	2.99	.76	5.39**	1.29
Error	15	.25		-.03		.24	
Flowering time with height							
Progenies	5			4.13	1.03		
Error	15			.01			
E-7 x 578							
Flowering time							
Progenies	5	55.42**	12.82	46.44	11.20	43.95**	9.18
Error	15	4.12		1.62		7.23	
Height							
Progenies	5	5.70**	1.26	4.02	.94	4.64**	1.05
Error	15	.67		.28		.44	
Flowering time with height							
Progenies	5			10.83	2.79		
Error	15			-.33			

**Significant at the .01 probability level.

Table 38. Mean squares and products, and variance and covariance components obtained from analyses of individual propagules of clones for flowering time and height of flowering stem

		Flowering time		Flowering time with height		Height of flowering stem	
	D.F.	Mean squares	Variance components	Mean products	Covariance components	mean squares	Variance components
533 x 578							
Clones	7	687.68**	39.33	195.92	11.32	148.80**	8.43
Propagules/clones	126	15.07		2.26		4.60	
540 x 578							
Clones	7	869.46**	51.44	77.87	4.93	34.43**	1.85
Propagules/clones	119	36.19		-2.03		4.46	
567 x 578							
Clones	7	784.07**	48.46	29.08	1.91	42.51**	2.39
Propagules/clones	117	8.64		-1.54		4.29	
E-7 x 578							
Clones	7	932.61**	58.88	379.99	24.37	188.88**	11.81
Propagules/clones	124	14.07		- .23		4.59	

**Significant at the .01 probability level.

Table 39. Mean squares and products, and variance and covariance components obtained from analyses of individual F_2 plants for flowering time and height of flowering stem

		Flowering time		Flowering time with height		Height of flowering stem	
	D.F.	Mean squares	Variance components	Mean products	Covariance components	Mean squares	Variance components
533 x 578							
Progenies	5	314.25**	1.97	-74.25	-.54	72.53**	.53
Plants/progenies	748	66.55		6.92		6.28	
540 x 578							
Progenies	5	271.72**	1.70	30.31	.20	7.24	-
Plants/progenies	736	61.38		5.28		6.04	
567 x 578							
Progenies	5	1,193.88**	8.67	291.77	2.17	179.61**	1.30
Plants/progenies	791	38.07		2.84		5.60	
E-7 x 578							
Progenies	5	1,285.04**	9.86	245.55	1.97	153.84**	1.19
Plants/progenies	742	65.06		2.03		6.21	

**Significant at the .01 probability level.

Table 40. Standard deviations, coefficients of variation, and observed correlations for flowering time and height in parental and F_1 sib-parental clones

	Standard deviations		Coefficients of variation		
	Flowering time	Height	Flowering time	Height	Observed correlation of flowering time with height
Family 533 x 578					
533	5.26	2.78	13.6	15.4	.350
578	3.68	2.48	18.0	26.4	.256
F_1 Sib-1	3.24	2.15	12.4	11.6	.508*
2	1.90	1.53	9.5	10.4	.541*
3	7.56	2.64	28.3	17.2	.518*
4	2.70	2.21	12.2	13.5	.302
5	2.70	1.27	10.1	7.2	-.055
6	1.24	1.67	6.8	12.3	.175
Family 540 x 578					
540	8.85	2.22	22.8	16.6	.160
578	2.24	2.24	12.9	22.8	-.068
F_1 Sib-1	11.05	2.11	38.5	21.3	-.405
2	8.41	2.53	35.9	26.9	-.553*
3	1.98	2.53	12.3	24.1	-.006
4	2.07	1.61	11.2	12.7	-.066
5	4.14	2.03	20.0	18.3	-.811**
6	2.74	2.57	11.7	23.4	-.809**

*Significant at the .05 probability level (n-2 D.F.).

**Significant at the .01 probability level (n-2 D.F.).

Table 40 (Continued).

	Standard deviations		Coefficients of variation		Observed correlation of flowering time with height
	Flowering time	Height	Flowering time	Height	
Family 567 x 578					
567	6.61	3.33	15.9	30.3	-.670
578	1.84	1.99	10.6	17.8	-.010
F_1 Sib -1	2.16	1.88	10.3	14.0	-.716**
2	2.22	2.17	12.3	21.2	-.250
3	2.23	1.78	11.5	17.8	-.100
4	4.03	1.85	23.0	15.9	.429
5	2.86	1.26	11.4	10.2	-.124
6	2.49	2.26	12.6	27.6	.134
Family 540 x 578					
E-7	3.07	3.25	8.0	16.8	-.657**
578	2.58	1.93	13.1	20.5	-.213
F_1 Sib-1	7.37	2.88	21.4	16.5	-.354
2	2.07	1.00	8.6	6.3	-.192
3	3.60	1.42	17.7	11.4	-.406
4	8.46	2.86	23.8	15.1	.266
5	2.96	2.30	13.4	16.2	-.416
6	1.72	1.30	8.7	9.8	-.120

Table 41. Replication variances and covariances, standard deviations of F_2 variances, and coefficients of variation for flowering time and height in F_2 progenies

	Replication variance[a]			Standard deviation of V_{F_2}		Coefficients of variation	
	Flowering time	Height	Replication covariance[b]	Flowering time	Height	Flowering time	Height
Family 533 x 578							
1 x 2	8.21	.05	-.32	7.52	2.90	26.3	19.6
3 x 4	9.05	.07	.71	7.59	2.56	26.0	17.0
5 x 6	12.04	.12	-.04	7.15	2.36	24.8	15.3
2 x 3	11.48	.08	.32	8.99	2.27	27.7	15.7
4 x 5	8.99	.02	-.06	6.15	2.36	21.8	14.3
6 x 1	7.76	.13	-.46	10.06	2.47	32.6	15.7
Family 540 x 578							
1 x 2	14.43	.03	.59	9.07	2.75	37.8	23.5
3 x 4	.07	.12	.05	7.66	2.11	37.5	18.8
5 x 6	4.58	.49	1.45	7.24	2.42	29.7	20.7
2 x 3	.51	.54	.32	7.38	2.40	34.8	20.7
4 x 5	6.74	.10	.61	6.69	2.53	30.1	21.3
6 x 1	2.58	.36	.86	7.73	2.25	35.4	19.4

[a]Total variance minus V_{F_2}.

[b]Total covariance of flowering time with height minus Cov_{F_2}.

Table 41 (Continued).

	Replication variance[a]			Standard deviation of V_{F_2}		Coefficients of variation	
	Flowering time	Height	Replication covariance[b]	Flowering time	Height	Flowering time	Height
Family 567 x 578							
1 x 2	17.06	.06	-.04	4.13	2.47	20.0	18.7
3 x 4	35.50	.21	.03	5.96	2.24	29.3	20.0
5 x 6	36.21	.15	.16	6.02	2.04	24.5	17.0
2 x 3	16.16	.21	-.25	4.02	2.45	20.3	22.9
4 x 5	77.02	.10	-.25	8.78	2.38	31.9	17.4
6 x 1	38.15	.51	.43	6.18	2.37	28.6	18.5
Family E-7 x 578							
1 x 2	19.55	.53	-3.12	7.77	2.78	23.5	18.3
3 x 4	13.65	.24	-1.37	8.71	2.22	30.1	15.6
5 x 6	4.38	.19	.23	7.48	2.26	31.7	15.8
2 x 3	1.00	.13	- .18	6.65	2.53	26.7	19.3
4 x 5	8.86	.45	- .14	8.64	2.46	30.4	15.1
6 x 1	21.94	.72	-3.92	7.64	2.33	26.5	15.8